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Review

# Lamprey fisheries: History, trends and management

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ABSTRACT

Three anadromous lamprey species support important commercial fisheries in the northern hemisphere, sea lamprey in the Iberian Peninsula and France, European river lamprey in the Baltic Sea countries and Russia, and Arctic lamprey in Russia. Pacific lamprey, Caspian lamprey, Korean lamprey and pouched lamprey are harvested for subsistence and local commerce on the Pacific coast of North America, and in Russia, China and Oceania, respectively. Habitat loss caused by human activities in rivers have reduced lamprey populations and collapsed most commercial fisheries worldwide. Overfishing is a concern because traditional fishing gears (e.g., pots, fyke nets) target lampreys during their upstream migration, usually in physical bottlenecks, which can result in exceedingly high fishing mortality. The reduction in catches has inflated lamprey prices and encouraged illegal fishing in certain countries (e.g., Portugal, Russia). The success of management actions for lamprey fisheries could be at risk due to knowledge gaps that still exist regarding stock structure, estimates of stage-specific mortality, distribution at sea, preferred hosts, and climate change impacts to the distribution and availability of adequate hosts. There is an urgent need for good-quality data from reported commercial landings and also from monitoring studies regarding the efficacy of mitigation and restoration efforts (e.g., habitat restoration, fishing regulations, artificial rearing and stocking). Involving the general public and stakeholders in the management and conservation of lampreys through outreach actions is crucial to promote the protection of the ecological and cultural values of lampreys and the understanding of their vulnerability.



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**Contents**



## Introduction

Lampreys are one of two living lineages of ancient jawless vertebrates which survived several mass extinction events and continue to adapt to a challenging environment where anthropogenic changes are occurring at a global scale (Docker et al., 2015). Lampreys have been harvested by humans for centuries, with the main species exploited being the parasitic, migratory species which attain larger body sizes (Renaud, 2011). Like many other fish species (e.g., salmon, shad) returning to rivers to spawn, migrant lampreys have high levels of fat in their body tissues, making them attractive to human and wildlife predators alike (Cochran, 2009). Only since the mid-20th Century have signs of overfishing emerged, most likely due to drastic reductions in population sizes, driven by the degradation of freshwater habitat, particularly, in the northern hemisphere (Maitland et al., 2015). Climate changes have aggravated conservation of lampreys due to habitat loss and/or degradation associated with damming, pollution, water abstraction, river flow regulation and overfishing (Clemens et al., this issue).

This review characterizes harvest activity for seven species of lamprey occurring in North America, Europe, Asia and Oceania: sea lamprey (*Petromyzon marinus* L.), European river lamprey (*Lampetra fluviatilis* L.), Pacific lamprey (*Entosphenus tridentatus* Richardson, 1836), Arctic lamprey (*Lethenteron camtschaticum* Tilesius, 1811), Caspian lamprey (*Caspiomyzon wagneri* Kessler, 1870), Korean lamprey (*Eudontomyzon morii* Berg, 1931) and pouched lamprey (*Geotria australis* Gray, 1851)).

Landings data resulting from commercial and/or subsistence harvest are not readily available, so we consulted a wide array of information sources, such as historical documents or local (often non-English language) fishery reports. Each of the seven species of lamprey is covered independently, with each section organized in a geographical context focusing on the cultural and socioeconomic importance, the identification of important fishing areas, the most common fishing gears and harvest techniques employed, and management actions that have been adopted.

The concluding part of the manuscript highlights the commonalities and differences across species and regions that can be drawn from this review, and points the way forward in terms of research for sustainable exploitation of this important halieutic resource.

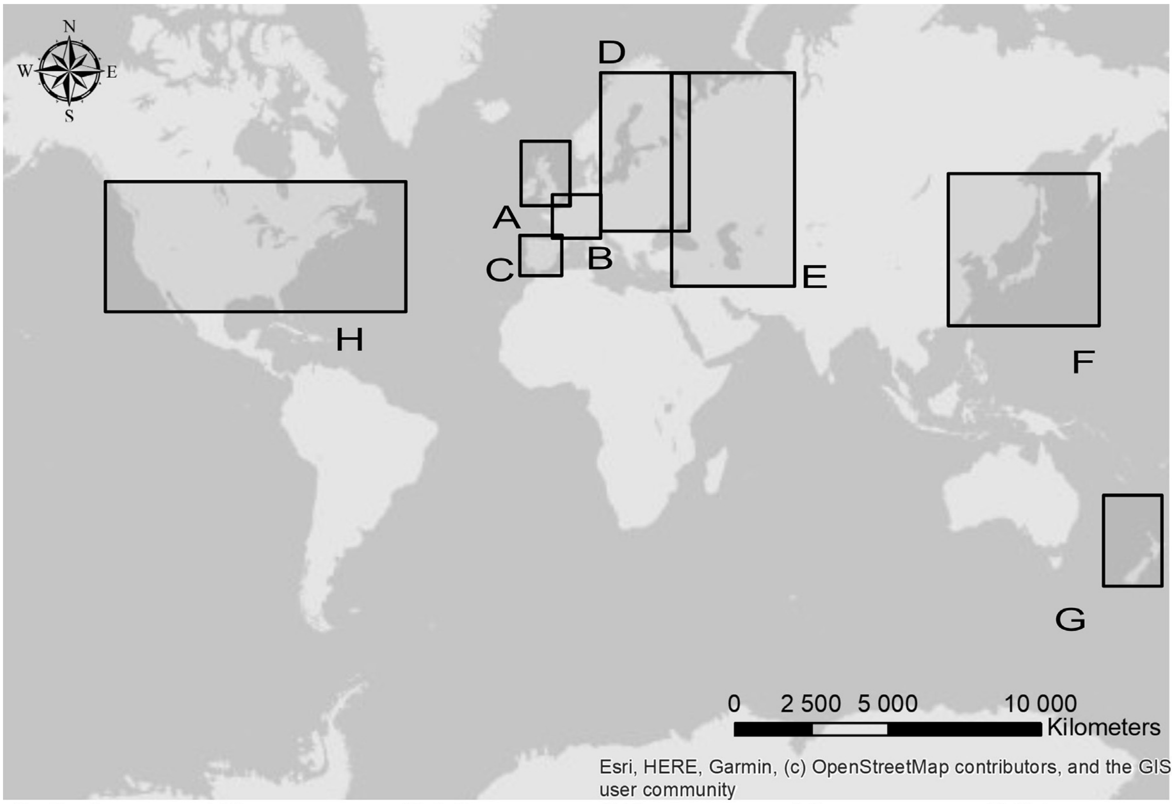
## Sea lamprey

In their native range, the sea lamprey is anadromous in western European and eastern North American river basins that drain to the northern Atlantic Ocean or western Mediterranean Sea (Renaud, 2011). It is the largest lamprey species, attaining more than 1.5 m length and over 2.5 kg in weight (P.R. Almeida, unpublished data). It supports important commercial fisheries in Portugal, Spain and France (Maitland et al., 2015).

In the Iberian Peninsula sea lamprey have been harvested for centuries and the importance of lamprey fisheries in this region is well documented, including disputes between fishermen and concession owners, the use of lamprey as payment, and the taxation of lamprey catches (Coelho, 1995; Silva, 2001; Hardisty, 2006; Docker et al., 2015). In the Minho and Galicia regions, there are to this day Roman-age stone foundations of lamprey traps constructed in river beds (Leite, 1999). In ancient Rome lamprey were a delicacy afforded only by rich people. Lamprey were preserved or taken live to Rome where they were a symbol of ostentation; prices ranged to 20 gold coins for one hundred lamprey (Fernandes, 2017). During the Middle Ages members of the nobility and some religious orders had fishing rights in some river stretches, where they used fishing weirs called "caneiros", specially constructed to harvest pre-spawning anadromous species (e.g., salmon, sea trout, shads, lamprey). At that time, both the king and the bishop received a portion of all the fish and lamprey caught; documents from 1291 show that this was a common practice (Baeta Neves et al., 1980).

We assume that lampreys were always a desirable commodity, but were they eaten by Christians long ago? The Bible affirms that "All that hath fins, and scales, as well in the sea, as in the rivers, and the pools, you shall eat. But whatsoever hath not fins and scales, of those things that move and live in the waters, shall be an abomination to you, and detestable. Their flesh you shall not eat: and their carcasses you shall avoid. All that have not fins and scales, in the waters, shall be unclean" (Book of Leviticus, Chapter 11, Verses 9 to 12). Certainly, mammals, crustaceans and molluscs fell into that scaleless category, as do lampreys. One thing we do know for sure, is that the traditional abstention from consumption of meat during Lent in the Christian liturgical calendar, promoted fish consumption throughout the peak migration period of lamprey and shads in the Iberian Peninsula.

The use of lamprey in traditional gastronomy increased their commercial value and led to an increase in fishing pressure. Presently, a single sea lamprey can easily reach 30–45 euros in Portugal (Andrade et al., 2007; Almeida et al., 2018). During the late 19th Century, official records show commercial fisheries for lamprey in all major Portuguese rivers, particularly in the central and northern regions of the country. During the second half of the 20th Century, the commercial value rose substantially until it reached the cur-




**Section A**
1-Severn
2-Thames
3-Welsh Dee
4-Humber Estuary
5-Yorkshire Ouse
6- Trent
7- Yorkshire Derwent
4-7 Humber River Basin

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3-Dordogne
4-Garrone
5-Rhone
6-Herault
7-Rhine
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**Section C**
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2-Tea
3-Minho
4-Lima
5-Cávado
6-Douro
7-Vouga
8-Mondego
9-Tagus
6-Guadiana

**Sextion D**
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2-Kalajoki
3-Perhonjoki
4-Lijoki
5-Oulujoki
6-Dalälven
7-Umeälven
8-Nemunas
9-Sventoji
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11-Daugava
12-Venta
13-Salaca
14-Narva
15-Pärnu
16-Jägala
17-Reiu
18-Ramametsa
19- Pirita
20-Kunda
21-Vääna
22-Seljia
23-Valgejõgi
24-Neva
25-Luga
26-Chernaya
27-Voronka
28-Sista
29-Kovashi
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10-Elva
11- Nes
12- Pechora
13-Usa
14- Ural
15-Volga
16- Sura
17-Alatyr
18-Barysh
19-Sviyaga
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**Section F**
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4-Aka
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7-Shinano
8-Machino
9-Han
10- Yalu
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12-Suchan

**Section G**
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4-Waikato
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6-Waitara
7-Patea
8-Waitotara
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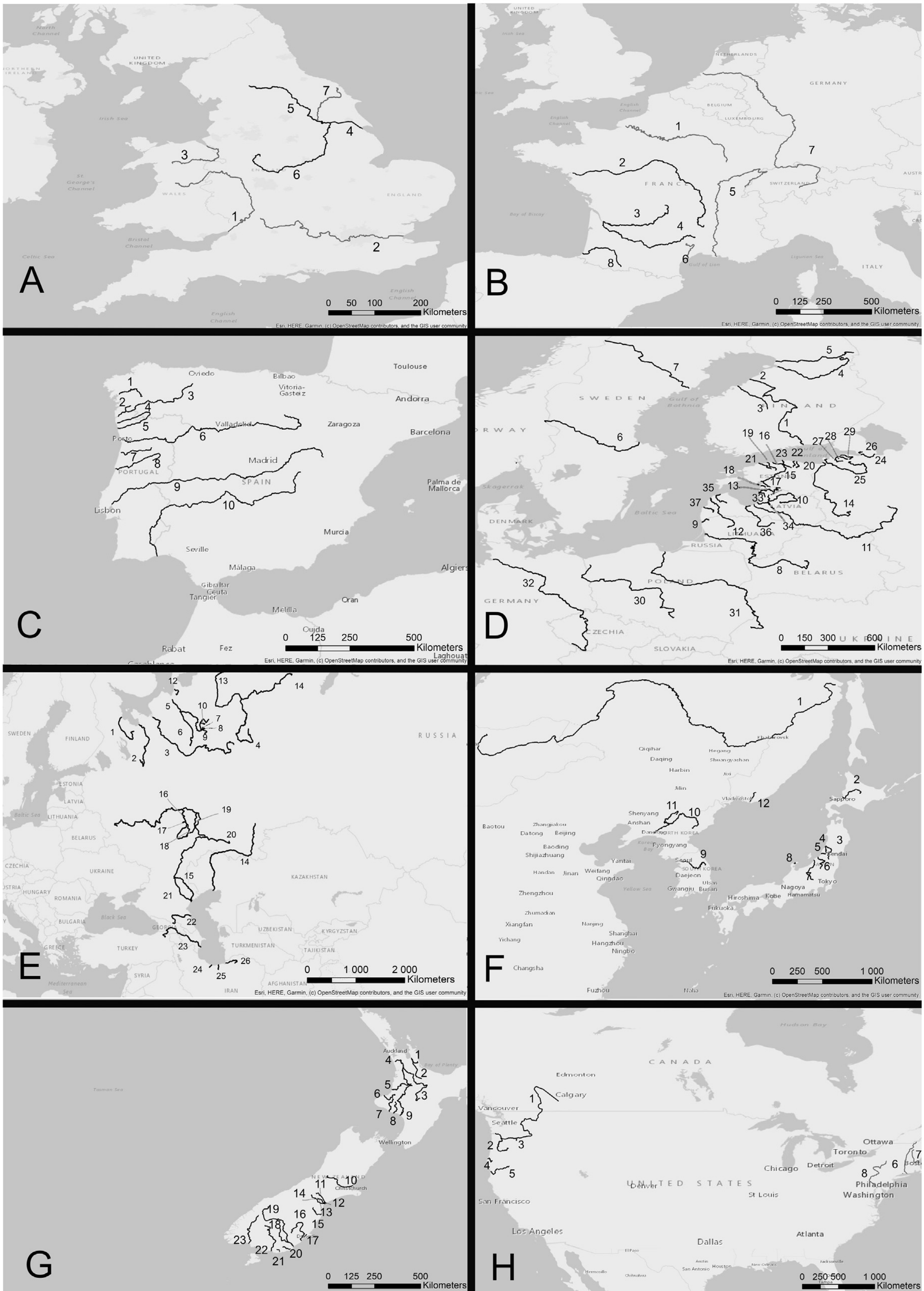
11-Orari
12-Ohapi
13-Temuka
14-Opihi
15-Waihao
16-Taieri
17-Silverstream
18-Pomahaka
19-Clutha
20-Catlins
21-Waikawa
22-Mataura
23-Waiau

**Section H**
1-Columbia
2-Willamette
3-Deschutte
4-Coquille
5- Klamath
6-Connecticut
7-Merrimack
8-Susquehanna

**a)**

**Fig. 1.** a) Location of the major lamprey fisheries around the world; b) detail of the rivers, mentioned in this manuscript, where commercial harvest occurs are represented in black and where it has ceased are identified in grey (global river hydrography and network routing obtained from Lehner and Grill, 2013).




**b)**

**Fig. 1.** (*continued*)

rent status of delicacy. Sea lamprey commands a high price, especially between February and April, during Lent and Easter (Andrade et al., 2007; Hardisty, 2006; Teixeira and Ribeiro, 2013; Docker et al., 2015). Dozens of gastronomic festivals take place every year in Portugal, during which hundreds of thousands of lamprey are consumed in many different ways, the most popular is a stew in its own blood served with rice. Some of the recipes are part of the Portuguese and Galician cultural heritage. The business involving lamprey justifies the annual import of thousands of sea lamprey from the Gironde system (Bordeaux, France). In Portugal and Spain, there are several brotherhoods devoted to the promotion of the cultural legacy associated with the gastronomic use of sea lamprey, and also to raise public awareness concerning sea lamprey conservation.

Sea lamprey populations are harvested commercially in several river basins of the Iberian Peninsula. On the Spanish coast, commercial fisheries are allowed only in the Ulla, Tea and Minho rivers, whereas in Portugal commercial harvesting takes place in the Minho, Lima, Cávado, Douro, Vouga, Mondego, Tagus and Guadiana rivers (Cobo, 2009; ICES, 2015) (Fig. 1).

Although a decrease in landings was reported at the end of the 19th Century, catches since have fluctuated (Baldaque da Silva, 1892; Mota et al., 2016), as shown in the official landings records at Caminha harbour in Minho River (Fig. 2). In fact, landings per fishing boat operating only in the Portuguese estuaries from the last 30 years (Source: DGRM, Directorate-General for Natural Resources, Safety and Maritime Services) show a decline in the last decade of the 20th Century to ca. 13 kg/boat in 1997. This was followed by a steady increase to ca. 158 kg/boat in 2016 due to either to an increase in sea lamprey abundance or, more likely, advances in fishing efficiency (Stratoudakis et al., 2016). This increase may also be the result of an improvement in the quality of landings records, or even a shifting target for artisanal fisheries (Mota et al., 2016).

Official records from commercial catches in freshwater are extensively underestimated and poaching is prevalent. Even though the available data is not ideal, it clearly shows that most of the Portuguese lamprey catch (ca. 85%) comes from the northern and central rivers (Minho, Lima, Vouga and Mondego rivers) identified as two distinct management units by Lança et al. (2014), thus requiring a separate management approach.

In France it is also quite possible that sea lamprey harvesting began many centuries ago. Official records refer to this fishery since the beginning of the 12th Century in the Loire watershed, during the 13th Century in the Seine River, and in the last quarter of the 16th Century in the Dordogne River basin (Pommeraye, 1662; Querrien, 2003; Yény, 2004). There are also references to the lamprey trade in the 15th and 16th centuries, for the Vierzon and La Rochele markets, respectively (Quero, 1998; Querrien, 2003).

As in the Iberian Peninsula, sea lamprey was considered a delicacy in France. In the 19th Century they were commonly eaten in the Rhine region (Anonymous, 1808). During medieval times, King John II regulated the trade of lamprey in Paris in 1350 (Blanchard, 1880), and in 1415 King Charles VI continued this protection (Millet, 1894), highlighting the importance of this fishery in France.

During the 18th Century French lamprey fisheries were reported in rivers draining to the Gulf of Biscay (Adour, Dordogne, Garonne and Loire rivers), and further north in the Seine River (Duhamel du Monceau and de La Marre, 1769; Roule, 1925). By that time, catches were also known in Mediterranean watersheds, namely, the Rhone, Rhine and Hérault rivers (Gervais et al., 1876; Reiber, 1888; Graffenauer, 1816) (Fig. 1). Although there is no reliable information about the quantities landed in the past, the Garonne, Loire and Rhone fisheries were considered the most important in France (Marchis, 1929; Fontaine, 1938). The decline in fishery landings, and most likely lamprey abundance, was noticeable in some French watersheds (e.g., Seine River) in the early 1900′s (Spillmann, 1961). At the end of the 20th Century, Castelnaud (2000) estimated that the total catch of sea lamprey from French commercial fishermen was 140 tonnes valued at three million euros. Presently, the harvest of this species is carried out only in three rivers: the Loire (58 tonnes), Garonne-Dordogne (75 tonnes) and Adour (7 tonnes).

Despite the variability in annual landings observed in the Gironde estuary since 1947 (50–200 tonnes, Fig. 3), there has been a positive trend in CPUE (catch per unit effort) since the end of the 20th Century (Beaulaton, 2008; Beaulaton et al., 2008; Lobry et al., 2016), broadly as described in Portugal. This may result from a recovery of these populations, or most likely, a reduction in the fishing pressure due to a decline in the number of fishermen (Beaulaton et al., 2008). Nevertheless, independent data from sur-

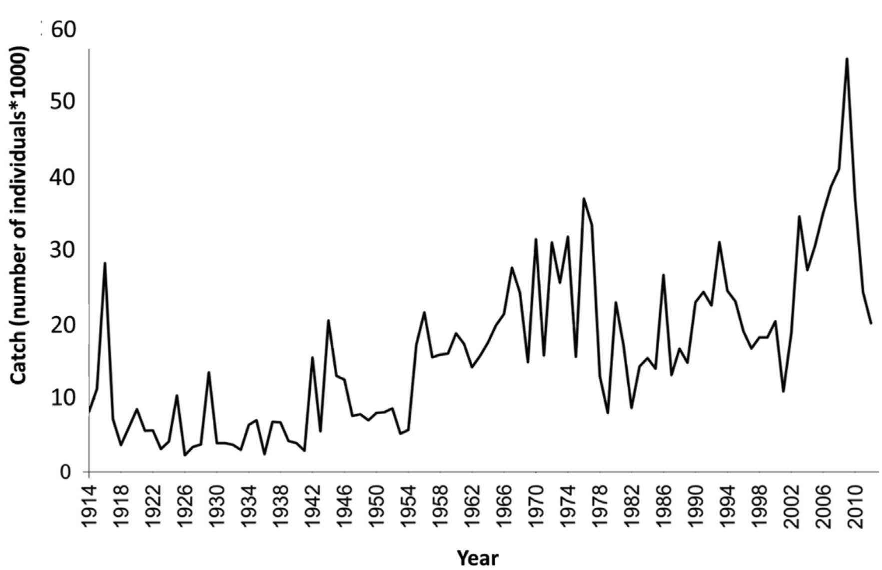



**Fig. 2.** Sea lamprey landings (number of individuals) at Caminha harbour (Minho River) by Portuguese fisherman (Source: National Maritime Authority; adapted from Mota et al. 2016), from 1914 to 2013.

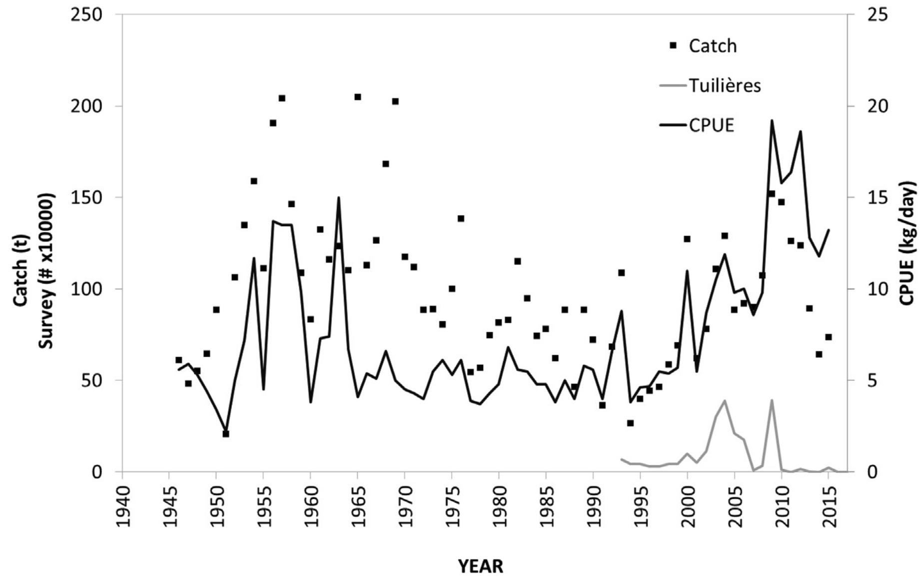



**Fig. 3.** Commercial sea lamprey catch(t), black squares,and CPUE (kg/day), black line, for trammel net fishers in the Gironde estuary (adapted from: Beaulaton, 2008; Beaulaton et al., 2008; Lobry et al., 2016), from 1946 to 2015. The grey line represents sea lamprey counts at Tuilières dam (#*10000) (Gracia et al., 2017), inbetween 1993 and 2017.

veys of a fish pass in the upstream reaches of the Garonne-Dordogne rivers show a dramatic decrease from tens of thousands of lamprey during the 2000s, to nearly zero at present (Gracia et al., 2017) (Fig. 3). This raises concerns about the sustainability of this fishery.

In North America sea lamprey was likely harvested as food by native people living on the Atlantic coast, although a survey of Tribal museums could not verify this idea. Scott and Crossman (1973) reported sea lamprey consumption was popular amongst European immigrants to North America. Local fisheries for migrant pre-spawning adults existed in the mainstem Connecticut and Merrimack rivers (Massachusetts), the Susquehanna River (Pennsylvania), and probably in many Atlantic coast rivers before mainstem dams were built in the 19th Century (Vladykov, 1949; Bigelow and Schroeder, 1953). Smith (1970) speculated that commercial fisheries for sea lamprey did not develop in Massachusetts because of the short time that migrant adults occurred at river mouths. Larvae rearing in the lower reaches of rivers have been harvested locally for fish bait, particularly in the Susquehanna River and other southern rivers (Bigelow and Schroeder, 1953).

While a few New England rivers (e.g., Merrimack, Connecticut) might have supported lamprey fisheries of local importance during the early half of the 19th Century, catch records are missing (Goode, 1884; Bailey, 1938; Bigelow and Schroeder, 1953). These fisheries likely ceased during the 19th Century, as dam construction in most rivers limited access of adults to upstream spawning and larval rearing habitat and abundance of sea lamprey decreased (Bigelow and Schroeder, 1953). Consequently, pre-spawning adults and larvae (for bait) were harvested mostly at or just downstream of dams in lower river mainstems or tributaries.

Across the species' geographical range, the type of gear used to catch sea lamprey depends mostly on local traditions and the characteristics of the fishing location. Some gears are and were commonly used in many European countries and North America, namely, trammel and gill nets, whether set or drifting, fyke nets and pots (Table 1; Duhamel du Monceau and de La Marre, 1769; ICES, 2015; Araújo et al., 2016). Fishing weirs were also an efficient technique used in North America and Europe (Pommeraye, 1662; Goode, 1884; Scott and Crossman, 1973), and there are also some ingenious methods of trapping lamprey in the Iberian Peninsula called "pesqueiras" (Fig. 4), that are still used in the upstream stretches of the Lima, Minho and Ulla rivers (ICES, 2015). These ancient stone structures were built into the river bed with notches where nets are placed. The fish enters voluntarily while swimming upstream, and these traps are visited daily to collect captured lamprey while leaving the gear set for several days or weeks (FAO, 2001–2019).

In the past, wounding instruments (various spears and hooked instruments) were often used to catch sea lamprey, although presently their use is allowed only in a few rivers in Portugal (Lima and Cávado rivers) and Spain (Tea River; Martins et al., 2015; Araújo et al., 2016).

In Portugal, by the end of the Middle Ages, the management of sea lamprey harvest mainly involved looking after the interests of higher social classes and the clergy, and solving disputes over the best fishing grounds (Anonymous, 1812). It is curious that documents from the 15th Century mention mostly problems with declines in allis shad (*Alosa alosa* L.; Anonymous, 1812), which could mean that in those days lamprey populations were abundant. Nevertheless, there are some references to stock depletion as a result of the methods and fishing gear employed. For instance, in the mid-17th Century restrictions to the mesh size used for lamprey and shads in the Lima River were enforced to avoid fisheries declines (Academia Real das Sciencias de Lisboa, 1815).

One of the major problems for fisheries managers today is the poor quality of catch data, mainly due to underreporting in inland fisheries (Stratoudakis et al., 2016). To overcome this problem in Portugal, independent monitoring actions (e.g., larvae abundance surveys in all Portuguese major rivers; visual counts of adults in the Coimbra dam fish pass in Mondego River) have been conducted to gather both biological and fisheries data. The latter are obtained through anonymous surveys conducted in all major Portuguese fishing communities (ICES, 2015; Almeida et al., 2016a, 2016b; Araújo et al., 2016), and after a few years, when trust is finally gained, the true landing numbers emerge.

Until about 2010, sea lamprey fisheries management in the Iberian Peninsula was based on technical measures with weak scientific support, great regional heterogeneity, and poor adaptability due to the lack of monitoring programs. Basically, those measures focused on the establishment of a fishing season (between January

**Table 1**
Gear types used to catch lamprey across their distribution range, per region and species, including both current and past methods of capture.

| Gear type (FAO classification) | | Sea lamprey | | | River lamprey | | | Pacific lamprey | Arctic lamprey | | Caspian lamprey | Korean lamprey | Pouched lamprey |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Iberian Peninsula | France | North America | France | Britain | Baltic Sea | North America | Japan | Russia | Caspian Sea | China | New Zealand |
| | Lifting nets | | *X | | | | X (Scoops; buckets) | X (Dipnet) | | X (Ice fishing) | X (ice fishing) | | |
| **Gillnets and entangling nets** | **Trammel nets** | X (Drift; Anchored) | X | | | | X | | | | | | |
| | **Gill nets** | X (Drift; Anchored; Fixed) | | | | | | | | | | | |
| **Traps** | **Fishing weirs** | X (Fishing weirs made of rock“Pesqueiras”) | *X | *X | *X | *X | X | | | | | | X (Fishing weirs made of wood: “Utu piharau”/“pā kanakana”; stone weir/whakaparu piharau) |
| | **Fyke nets** | X (“Botirão”; “Camboa”) | *X | | | X | X | | X | | X (Wicker nets) | X (“Yu Zhu” net) | X (“Hinaki” nets; fyke nets) |
| | **Pots** | | X | | X | X | X | | | | | | |
| | **Traps** | | *X | | *X | *X (Putchers; weels) | X (Baskets; logs; cone traps; traps) | X | X (Cylindrical basket traps) | X (Bottom minnow traps: meshed “Ryuzhi” ; baskets with spikes) | | | X (Barriers made of small branches across low shingle rivers; different types of traps made of bundle of bracken) |
| **Seine nets** | **Beach Seine Nets** | | *X | | | | | | | | | | |
| **Grappling and Wounding Gears** | **Harpoons** | X (Rods crowned with barbed hooks “Galheiro” larger rod; “Bicheiro” smaller rod) | | | | | | | X (Rods equiped with a hook; harpoons) | X (Wooden hooks; sickels/ice fishing) | | | X (Long rods equiped with a hook; rods crowned with barbed hooks) |
| | **Spears** | | *X | | | | | | | | | | |
| | **Rakes** | X (“Fisga”) | | | | | | | | | | | |
| | **Pincer** | | *X | | | | | | | | | | |
| **Other Gear** | | | *X (Harvesting machine “baro”) | | | | | | | | | | |
| **By hand** | | X | | X | | | | X | X | | X | | x |

*No longer used.

**Fig. 4.** Fishing weirs ("pesqueiras") in Lima River. The white arrow shows the slots where the traps are placed (see detail in the left corner) (Photo "pesqueira": B.Quintella; photo fisherman: G.Cardoso).

and April), defining fishing gear, regulating the maximum number of fishing licenses and a minimum landing size (Araújo et al., 2016).

Nowadays, things have changed, for instance in the Mondego River (Portugal) a pilot project devoted to the integrated management of sea lamprey and allis shad fisheries was implemented in 2013, along with strong investment in habitat restoration and research. This project engaged stakeholders in the decision process, encouraging meetings between commercial fishermen, scientists, and the authorities responsible for fisheries legislation (Almeida et al., 2016b). The resulting fishing restrictions were imposed to promote stock recovery and recolonization of newly-accessible upstream habitat (Moser et al., this issue). The restrictions included a shorter fishing season and an intermediate fishing closure for lamprey and shad so that river and estuary are net free for a few days during the peak of migration (10 days in 2013, the first year and 5 days in the following years, Stratoudakis et al., 2016). A positive response of the sea lamprey population was observed, with a peak in dam passage immediately after the fishing closure in 2014 and an increase in upstream larval abundance in the following ears (Almeida et al., 2016a; Pereira et al., 2017).

While at first these restrictions caused some conflict, fishermen subsequently embraced the new management scheme after seeing its undeniable positive impact on sea lamprey larval abundance. The approach taken in the Mondego River is currently being replicated in other Portuguese rivers (e.g., Vouga River), which have similar problems and where fishermen acknowledge the need for a similar management approach (Almeida et al., 2018).

In contrast, lamprey fishing in France is mainly regulated through regional committees for the management of diadromous fish ("COGEPOMI - COmité de Gestion des POissons MIgrateurs"). These committees gather administrators, commercial and recreational fishermen, other private stakeholders (e.g., hydropower companies), local representatives and scientific institutions to decide on a diadromous fish management plan ("PLAGEPOMI - PLAn de GEstion des POissons MIgrateurs"). Fishing regulations for lamprey harvest are based on seasonal and weekly closures, control of gear characteristics, and limiting the number of fishermen. Although fishing mortality of sea lamprey has never been assessed, a preliminary mark-recapture study in the Gironde estuary found that 27% of the tagged marked lamprey were recaptured by fishermen (Anonymous, 1979).

Because there are no commercial fisheries for anadromous sea lamprey in North America, the management of anadromous sea lamprey populations is implemented from a conservation perspective. A restoration/management plan for anadromous sea lamprey in the Connecticut River was approved in 2018 by the Connecticut River Atlantic Salmon Commission (CRASC, 2018). The plan contains programs to improve adult passage at dams, identify tributaries with nesting and rearing reaches, and monitor annual adult migrants and nesting. This Plan is the first management plan for anadromous sea lamprey in any North American Atlantic coastal river.

Due to the great contribution of anadromous sea lamprey to Atlantic coast stream ecology and production of fish species important to fisheries, like Atlantic salmon, *Salmo salar* (Saunders et al., 2006; Nislow and Kynard, 2009), all coastal states (USA) and provinces (Canada) with native anadromous sea lamprey are encouraged to implement restoration programs.

## European river lamprey

European river lamprey (hereafter river lamprey) is a smaller, normally anadromous lamprey that can reach 490 mm in length and 150 g in weight, with a distribution range from southern Norway to France, including Ireland and the UK, the Baltic Sea drainages, Portugal (Tagus River) and Italy (Arno and Tiber rivers; Renaud, 2011).

Historically, fishing for lampreys was common in most of France (Belon du Mans, 1555; Gervais et al., 1876; Roule, 1925; Spillmann, 1961), but river lamprey was not landed in large amounts (Blanchard, 1880; De La Blanchère, 1880). This species was consumed in January and February (Reiber, 1891), and was provided for King John IV of Britany for Christmas 1377 (Le Moyne de la Borderie, 1906). River lamprey was harvested from the Seine and Loire rivers (Duhamel du Monceau and de La Marre, 1769) and in the Languedoc region (Gervais et al. 1876) (Fig. 1). Records from 1871 for the Dordogne River in the Libourne district reported a catch of 30,000 river lamprey, but nowadays this species is considered rare in the Garonne-Dordogne watershed and harvest is restricted to the lower parts of these rivers (Castelnaud, 2000; Ducasse and Leprince, 1980; Guérault et al., 1994). Official commercial and recreational landings from 1999 to 2002 ranged between 300 and 4600 kg, but there is likely some confusion with sea lamprey (Anonymous, 2004). Although Taverny and Élie (2010) stated that river lamprey fisheries ended in the 1980s, it is reasonable to assume that a small fishery still targets this species in France.

In Britain, river lamprey was undoubtedly captured alongside other fish species in medieval times at numerous fish weirs and keratinous lamprey teeth have been found in English archaeological remains (Wheeler and Jones, 1989). Lamprey (river and sea) was a favoured dish among common people and at banquets of nobles. Famously, King Henry I apparently died from eating an excess of lamprey in France in 1135, but it is unclear whether they were directly to blame (Green, 2006). The chronicler Henry of Huntingdon reports that the king was healthy in autumn 1135, but died about a week after eating a "surfeit of lampreys" in the last week of November. Given that sea lamprey adults migrate upstream in spring, he likely ate river lamprey. Presentation of lamprey in pies at medieval English Royal events is well reported. In 1200, King John fined the city of Gloucester, on the Severn River, 40 marks (over USD 400,000 today) for forgetting to send him a lamprey pie at Christmas (Skinner, 2012). This custom died out, but Queen Elizabeth II received a lamprey pie for the 1952 Coronation and for her Silver Jubilee in 1977 (Renaud, 2011).

In the UK, river lamprey is perhaps best known as fishing bait. Their larvae, often referred to as 'prides' are recorded as being used as bait for angling since the 17th Century (Walton, 1653; Buller and Falkus, 1994) but are little used today. From the 1700s, fishing for sub-adult river lamprey in Britain shifted from capture for food towards capture as fishing bait for commercial long line fisheries, particularly in the North Sea, (Beaufoy, 1786). They were favoured as long lining bait, in part, because of their toughness on the hook. Landings of river lamprey were mainly from the rivers Severn, Thames, Welsh Dee, and several rivers in the Humber river basin (Fig. 1) (Beaufoy, 1786; Anonymous, 1865; Buckland and Walpole, 1873; Smith, 1912; Spicer, 1937; Hardisty, 1986; Buller and Falkus, 1994; Masters et al., 2006). Today the only licensed fisheries for river lamprey in the UK are on the Yorkshire Ouse and Trent (Humber basin). In the 1780s several hundred thousand adult river lamprey were caught each year for bait (Beaufoy, 1786). In the Thames fishery alone, which employed 30–40 seasonal lamprey fishers, over 300,000 lamprey per annum were caught and sold for 2–4 Guineas per thousand (Beaufoy, 1786). An increasingly large proportion of the catch was sold to the Dutch and transported in live wells on boats to Holland, resulting in a doubling in the price, an increase in pressure on the fishery, and geographic expansion to the Ouse, Trent and Severn rivers (Anonymous, 1865; Smith, 1912). According to Renaud (2011), up to 450,000 adults were used as bait by the English fishing fleet annually in the 19th Century, and Hardisty (1986) suggests the peak annual catch may have been as high as a million river lamprey. By the late 1800s, with increasing pollution, more river barriers and exploitation (despite implementation of a 30 March-23 August fishery closure) the Thames river lamprey fishery was declining, with catches falling from a norm of over 200,000 per annum to 80,000 in 1863, 25,000 in 1864 and 6000 in 1865 (Anonymous, 1865).

River lamprey continued to be landed from the Humber drainage during the late 19th and early 20th Centuries. On the Trent, over 10,000 river lamprey caught in one night were sold for £10 per thousand individuals (Spicer, 1937). On the Yorkshire Ouse in 1908–1914 river lamprey were caught in a single putcher (woven basket with funnels) placed in a gap in the weir at the tidal limit (Appleby and Smith, 2000) and catches were 25,000–54,000 lamprey per season (Masters et al., 2006). As the North Sea long line fishery was replaced by trawlers in the early 20th Century, lamprey fisheries in Britain died out (Lanzing, 1959), but most stocks were probably already depleted due to pollution and the proliferation of river barriers (Hardisty, 1986).

In the late 1980s and early 1990s, adult river lamprey from bycatch in commercial eel (*Anguilla anguilla* L.) traps in the Humber river basin was popularized as a successful bait for northern pike (*Esox lucius* L.) and other predatory fishes, and this created a new market (Masters et al., 2006; Foulds and Lucas, 2014).

Before 2011, lamprey catch records from the eel fishery were voluntary and minimal in detail, but carefully recorded since, in terms of catch, landings and effort. For the tidal Ouse in 1995–2016, total annual landings averaged about 19,600 lamprey. Almost all of these entered the UK angling bait market.

Using an anonymous survey of wholesalers supplying angling shops, Foulds and Lucas (2014) discovered that reported landings from the Ouse were only a fraction of the UK river lamprey bait market for angling. For the year 2011–2012, of 9 tonnes of river lamprey sold they estimated that about 51–68% of lamprey bait sold in Britain came from the Netherlands, 14–31% from Britain and 18% from Estonia. Dutch lamprey came from Dutch eel bycatch, but this fishery ended with regulatory tightening in 2014 (Foulds and Lucas, 2014). Estonian lamprey continue to be imported to the UK lamprey bait market.

Although river lamprey harvesting was known in several Baltic countries, its importance as a commercial fishery substantially declined during the 20th Century. In Poland an apparent gradual lamprey population decline was observed in the Oder, Vistula and Elbe rivers (Fig. 1), with annual catches in the lower Vistula River of ca.70 tonnes after World War II (WW II) declining to below one tonne by the end of the 1980s (Witkowski, 1996; Hanel and Andreska, 2016).

River lamprey fishing records in Finland go back to the 15th Century, at the latest (Tuomi-Nikula, 1981). The right to catch lampreys was associated with land ownership (Storå, 1978; Tuomi-Nikula, 1981) and was mainly the privilege of wealthy landowners, who gained extra income by selling lampreys (Tuomi-Nikula, 1981). They had the right to use "basket-channels" constructed in riffle areas, which were inherited as part of the property. This practice was still common in the 19th and early 20th centuries. Lamprey was a delicacy of wealthy people especially in cities (Tuomi-Nikula, 1981; Storå, 1978), but they were also consumed by fishermen (Storå, 1978; Hiltunen et al., 2013). The importance of river lamprey in the domestic economy of the peasantry was probably limited (Storå, 1978).

When the number of professional fishermen increased at the beginning of the 20th Century, they gained lamprey fishing rights (Tuomi-Nikula, 1981). By the 1960s, river lamprey were mainly caught by commercial fishermen or people who, alongside their main occupation, earned some extra income from lamprey (Tuomi-Nikula, 1981). In the early 2000s, the majority of the Finnish lamprey fishermen said that they caught lamprey for household use, but also sold a proportion which, on average accounted for 5% of their annual income (Katajisto, 2001).

Currently, there is at least one small lamprey processing company by the river mouth of almost every larger river entering the Bothnian Bay (Kaski and Oikarinen, 2011). There are also some larger processing companies, which buy lamprey from different fishing zones (Hiltunen et al., 2013). Most of the lamprey products are traded to local people or tourists directly (Kaski and Oikarinen, 2011). There are annual lamprey festivals in at least two cities and lamprey is part of other fish festivals organized along the west coast of Finland. River lamprey are prepared in many different ways in Finland (Tuomi-Nikula, 1977), but currently charcoal grilling is most popular (Kaski and Oikarinen, 2011; Saulamo, 2005).

The total river lamprey catch in Finland has declined progressively since the early 1970s from 2.7 to 3.0 million lamprey in 1970, to 2.0–2.5 M in 1980, and 1.8–2.5 M in 1988 (Tuunainen et al., 1980; Mäkelä and Kokko, 1990). In the early 2000s, the average annual catch was estimated to be only 1.1 M lamprey (Kaski and Oikarinen, 2011) and in 2006–2010, ca. 0.9 M specimens (Hiltunen et al., 2013). A long term study for the Kalajoki and Perhonjoki rivers showed that both the total catch and the number of upstream migrating river lampreys have decreased since the early 1980s (Vikström, 2018; Aronsuu et al., 2019; Laitala, 2019, Fig. 5). Since 2010, at least in Kalajoki River, the numbers of spawning adults showed a slight increase (Laitala, 2019, Fig. 5), which could reflect a reduction in fishing effort.

In Finland the catch of river lamprey varies from year to year, but a decreasing trend has been detected in most rivers during recent decades (Hiltunen et al., 2013). The decline has been especially dramatic in dammed rivers. For example, the yearly catch before damming in the rivers Iijoki and Oulujoki was estimated to be at least 500,000 individuals (Fig. 1). Four decades after damming (i.e., 2006–2010), it was only 100,000–150,000 individuals in the Iijoki River and less than 100,000 in the Oulujoki River (Hiltunen et al., 2013).

Almost 90% of the Finnish river lamprey catch is harvested from rivers entering the Bothnian Bay (Hiltunen et al., 2013) and lamprey fishing is not practiced as much in the southern parts of Finland (Ruuskanen, 2003; Saulamo, 2005). However, approximately 100,000–200,000 lamprey, estimated to be 10% of the total run, are caught yearly from the Kymijoki River, the largest river entering the Gulf of Finland (Fig. 1b) (Saulamo, 2005). In other rivers entering the Bothnian Bay, the fishing mortality may exceed 60% in some years (Aronsuu et al., 2019). The exact number of fishermen in Finland is not known, but Aronsuu (2011) estimated that in the 2010s there were ca. 400 lamprey fishermen.

In Sweden, the earliest records of lamprey fishing date back to 1425 (Sjöberg, 2011) and the history of Swedish lamprey catching is very much the same as in Finland (Storå, 1978). The tradition of lamprey fishing has regressed during the last decades (Sjöberg, 2011), with only the elderly generations catching lamprey for private consumption nowadays. During the 1940s and early 1950s, the average yearly catches from 25 rivers were around 200,000

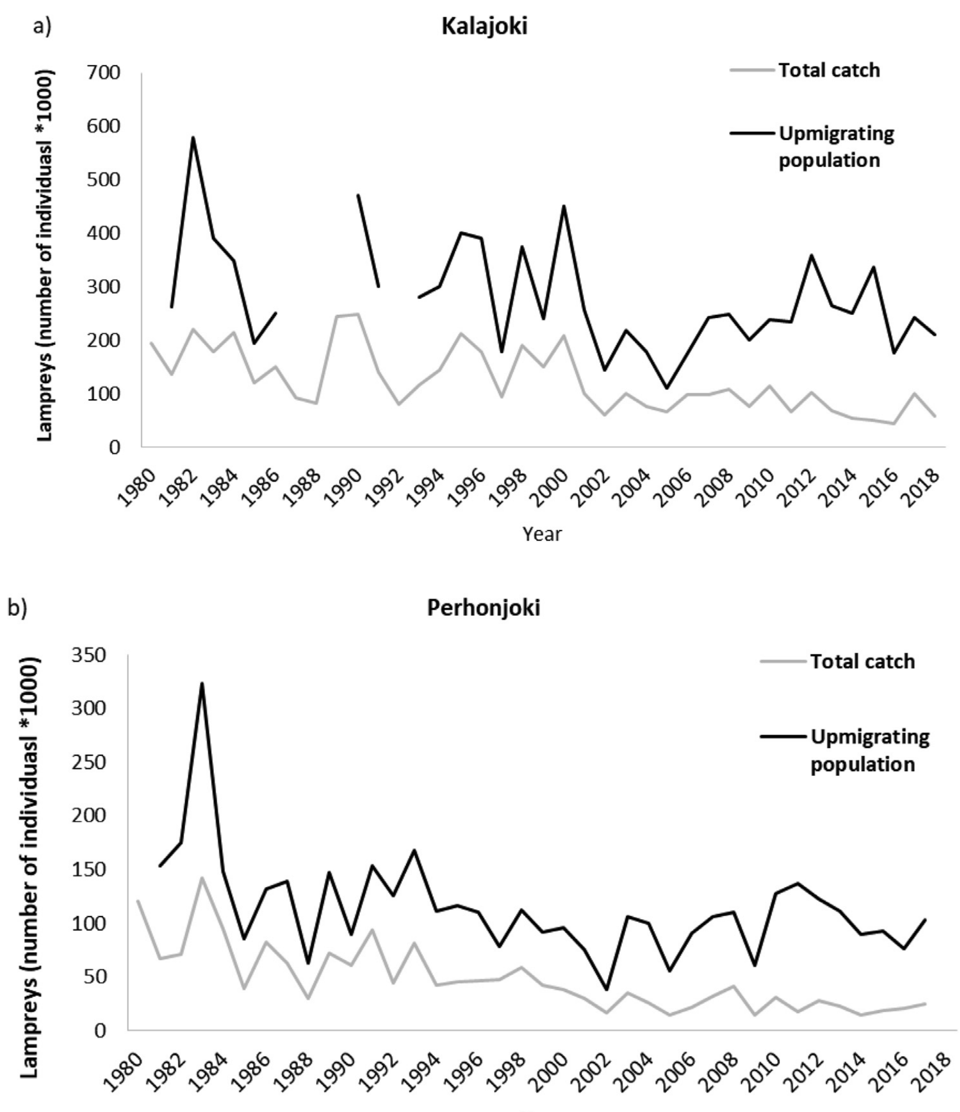



**Fig. 5.** Estimated numbers of upstream migrating lampreys, in black, and the total lamprey, in grey, catches (number of individuals) in the Finnish rivers a) Kalajoki and b) Perhonjoki, from 1980 to 2018. Modified from Vikström (2018) and Laitala (2019).

river lamprey, mostly from the biggest rivers (e.g., Dalälven, Umeälven rivers) (Fig. 1b) (Sjöberg, 2011). The total annual catch in 1993–2003 was 220,000 and 380,000, whereas in 2010–2011 it decreased to ca. 150 000 specimens (Sjöberg, 2011). Lamprey fishing exists in most of the tributaries from the Dalälven River northwards; but by 2010–2011 lamprey fishing was confined to about 14 Swedish rivers and involved a total of only 50–55 fishermen (Sjöberg, 2011). Lamprey fisheries largely ceased in most rivers that were dammed for hydropower (Sjöberg, 2011), and Swedish fishermen did not adopt new fishing methods in heavily modified rivers as had fishermen in Finland. The total catch in Sweden may not accurately reflect changes in lamprey abundances because the fishery is currently at a very low level (active in only five rivers), but one may assume that the causes for the reduction in river lamprey abundance in Sweden, are the same as previously mentioned for Finland (Sjöberg, 2011).

River lamprey was highly valued also in Prussian Lithuania, and has been an important fishery target over the last centuries. At the end of summer in Tilžė (currently Sovetsk in Kaliningrad Oblast) and Klaipėda town restaurants and taverns raised flags with seven or nine dots to indicate that river lamprey were ready to be served (Bittens, 1913). River lamprey were usually grilled over low heat on peat blocks to preserve their fat. In taverns, lamprey were served in big bowls, and the price was calculated according to the number of heads left on plates. Exports to Germany were smoked and marinated in oil or beer vinegar. The smokehouses sometimes processed up to 20 tonnes of lamprey a week. However, after WW II this gastronomic tradition disappeared.

Lamprey fishing is strictly regulated in Lithuania by quotas, fishing gear limits and/or fishery closures. The quota for the Šventoji River is 1.5 tonnes and in the Nemunas River Delta it is 2 tonnes (Fig. 1b). Therefore total catches in Lithuania in the period 2010–2019 have been quite small, on average 5 tonnes (ranging from 2 – 6.2 tonnes). Even so they have increased in comparison to 2000–2009 when the mean annual catch was 3.5 tonnes (Kesminas and Švagždys, 2010). However, those catches are still well below the catches of late 19th and early 20th Century, when on average 77 500 individuals (ca. 7.8 tonnes) were caught in the Curonian Lagoon. A peak was reached in 1930–1935, with a reported catch of 30–53 tonnes per year (Gaigalas, 1965). After WW II, lamprey fisheries resumed only in the 1960s with a mean annual catch of 3.7 tonnes remaining stable in the 1970s but reducing to an annual average of 0.5 tonnes per annum in the – 1980s. After independence in the 1990s, lamprey fishing resumed, but with quite small reported catches. The unexpectedly high catch of 12.3 tonnes in 1995 accounted for 55% of the landings for this decade (Fig. 6) (Virbickas, et al., 1996; Kesminas and Švagždys, 2010).

In Lithuania, river lamprey are commercially fished in the River Šventoji, the Nemunas River Delta and the Curonian Lagoon (Fig. 1b), the latter being the main fishing ground. Since 2010, catches from this lagoon comprise 65% (range 42.2–90.5%) of the total annual catch. Fishing grounds in the Nemunas and Šventoji rivers are located close to the river mouths, so catches are greatly affected by hydrological conditions during the fishing period. There have been attempts to fish for lamprey in the upper reaches of the Nemunas River, just below the Kaunas hydroelectric power plant, but this fishing ground was used only in 1966 (Maniukas and Mackevičius, 1966).

Although the artisanal lamprey fisheries in Latvia and Estonia also suffered after WW II, they recovered and have sustained their importance. Latvia has its own processing traditions, which include smoked lamprey in cans or grilled lamprey in a mustard marinade or jelly. Records from the 19th Century indicate that lamprey were caught and grilled in the Gauja Estuary (near Carnikava). As a result, today Carnikava is called the "Kingdom of the lamprey" and the lamprey is depicted in the county's coat of arms. Nowadays Latvian fishing communities organize lamprey festivals for the public that include thematic exhibitions, display of lamprey capture methods and tasting of lamprey dishes. The biggest and best known is the Carnikava festival, which is celebrated on the penultimate Saturday of August, when the Carnikava lamprey fishing season opens.

The Latvian river lamprey fishery represents on average 25% (range 17–31%) of the country's total inland fisheries landings (Riekstiņš et al., 2018). During the 1950s, the mean annual catch of river lamprey was 75 tonnes (Ryapolova, 1960), increasing to 241.3 tonnes per annum for the period 1960–1977 (Birzaks et al., 2011). This period was followed by a sharp decline in landings, probably due to exceptional productivity of the cod (*Gadus morhua* L.) stocks in the Baltic Sea during 1976 and 1977 and associated predatory impact on river lamprey (Birzaks and Abersons, 2011). The lowest recorded catch (8 tonnes) during this period occurred in 1980 (Fig. 7) (Riekstiņš et al., 2010). After the decline, mean

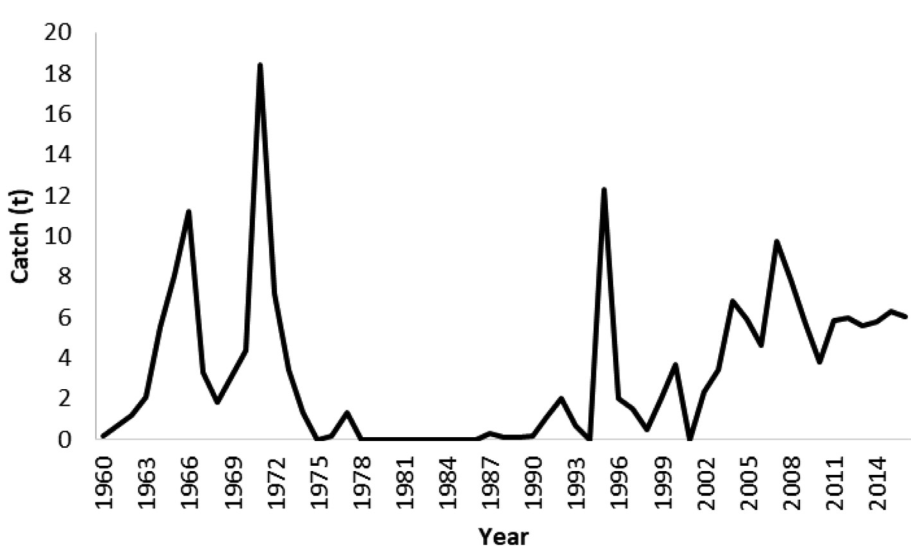



**Fig. 6.** River lamprey harvest (t) in Lithuania, from 1960 to 2016.

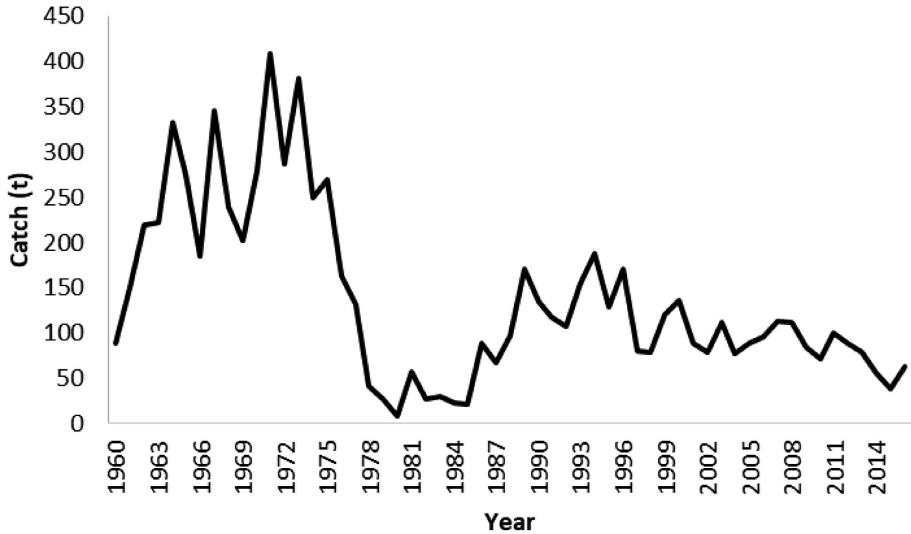



**Fig. 7.** River lamprey harvest (t) in Latvia, from 1960 to 2016.

annual catches recovered to 59, 128 and 99 tonnes in the 1980s, 1990s and 2000s, respectively. In recent years, the mean annual catch is ca. 67 tonnes (Riekstiņš et al., 2018).

Until 1991, the number of Latvian rivers where river lamprey were harvested dropped to 10, but after the restoration of Latvia's independence, every resident of Latvia was entitled to fish. Therefore, between 1992 and 2002, the number of fishermen increased substantially, and fishing for lamprey in small rivers resumed (Birzaks, 2007). At the moment, commercial fishing for river lamprey is permitted in 17 rivers. The most important annual landings come from the fishing grounds located on the largest Latvian rivers (i.e., Gauja, Daugava, Venta, Salaca rivers), and the contribution of each river varies from 10.4% to 36.5% of the total annual catch (Abersons and Birzaks, 2014).

In the 19th and 20th centuries in Estonia, grilled lamprey were mainly marinated in wooden barrels. The marinade was a brine of wine vinegar, peppers, nutmeg and bay leaves. Marinated lamprey were purchased by Russian fishmongers and later sold in Narva for as much as two kopecks each. As in Latvia, Estonia has a festival devoted to lamprey that occurs in Narva-Jõesuu at the end of September.

Over the last 50 years, the catch of river lamprey in Estonia ranged between 3 and 68 tonnes per year. During the period 1928–1938 the annual catch averaged 67 tonnes (range 41–102 tonnes), between 1969 and 1983 it was ca. 26 tonnes (range 3–68 tonnes), and between 1992 and 1999 it was ca. 10 tonnes (range 1–25 tonnes). Since the 2000s, the river lamprey catch has been relatively stable (25–66 tonnes per year; Baikov et al, 2017).

The most important Estonian river lamprey spawning population migrates into the Narva River which discharges into the Gulf of Finland, and the Pärnu River in the Gulf of Riga (Baikov et al., 2017). About 95% of Estonia's total catch comes from the Narva, Pärnu, Jägala, Reiu, Rannametsa, Pirita, Kunda, Vääna, Selja and Valgejõgi rivers (Fig. 1b). However, since 2008 the largest proportion of the country's catch (73.1%, range 58.5–82.3%) is harvested in the Narva River (Armulik and Sirp, 2017).

In pre-Petrine Russia, the lamprey was called "vyun" (crinkling), and only in the the Baltic Sea basin (and on the Volga River) the name of "minoga" was used, apparently taken by the Slavs from the Latvian-Lithuanian and Finnish languages. River lamprey in the eastern Gulf of Finland has been valued as a delicacy and has been known since at least the 18th Century (Kuderski, 2007). Lamprey caught at the mouth of the Neva River were immediately given to the "lamprey-men", who plunged the live lamprey into a weak brine and laid them out in rows on iron trellised braziers. The cooked lamprey were placed in barrels and doused with vinegar, pepper and bay leaf (Bril, 2008). This species gained significant commercial importance with the development of the former USSR fishing industry in the Leningrad Region after the 1920s, continued during the 20th Century, and was interrupted only during WW II. In some years, the catch of river lamprey in the Gulf of Finland exceeded 100 tonnes. However, catches were often lower, resulting from both rapid fluctuation in apparent abundance and economic crises that impacted fishing activity (Kuderski, 2007). River lamprey is used locally fresh in the fall and early winter. The local industry is also focused on the manufacturing of various canned products, sold throughout Russia and Estonia. In Staraya Ladoga and Ivangorodskaya Krepost lamprey entered the local folklore as a proverb: "You haven't been to Ivangorod, if you didn't eat a lamprey there". River lamprey is also one of the three symbols of the medieval town of Vyborg (Anonymous, 2018). In the Soviet and modern Russia, lamprey is included on the menus of official dinners and formal receptions in the Kremlin to celebrate the special occasions or international visits (Vasilieva, 2015).

From the 16th century reports "on the supply of eel from the Narva River to the tsar table", it is known that the Narva River supported lamprey fishing (as is common in many historical accounts "eel" often refers to lamprey – both having long eel-shaped bodies). During the reign of Catherine II (18th Century), there was a community of Russified Finns on the shores of the Gulf of Finland and Podzorny Island, who were exclusively engaged in fishing and preparing lampreys. In those days lamprey fishing was done in the spring, after the boat navigation reopened, when up to 10,000 pots ("burak" or "morda") operating at the same time were set over night in the Neva River mouth (Bril, 2008).

In addition to development of lamprey fisheries in the Baltic during the 19th Century, there was also harvesting of Caspian lamprey in the Caspian region and Volga River (Kuznetsov, 1902). Presently the main Russian fishing areas in Baltic region are the Neva, Luga, Narva, Chernaya, Voronka, Sista, Kovash rivers (Fig. 1b). The proportion of river lamprey in the total catch of the Neva River may reach 7.03% (Luzanskaya, 1940; Gusev, 1968), and during the last few decades river lamprey and smelt (*Osmerus eperlanus* (L.)) have been the main fishery targets (Kuderski, 1996) (Fig. 8).

As for other lamprey species, fishing gear for river lamprey varies according to the fishing location and traditions. Over time, the

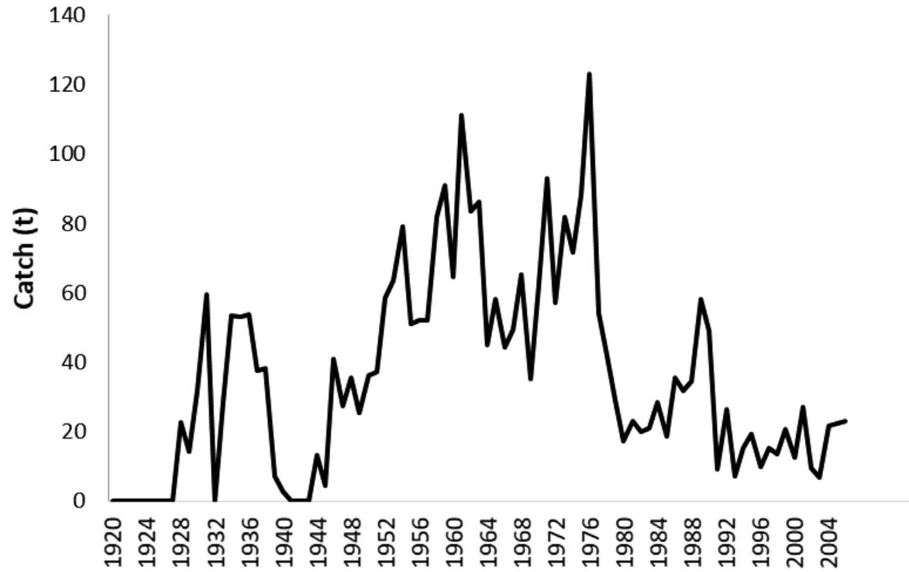



**Fig. 8.** River lamprey harvest (t) in Russia (rivers Neva, Luga, Narva, Chernaya, Sista, Kovash and Voronka), from 1920 to 2006.

architecture of the main fishing gears has not changed significantly, but natural materials have been replaced by plastic components and artificial fibres (Table 1).

In Britain, lampreys, especially river lamprey or 'lampern', were caught in traditional baskets, known as putcheons/putchers and weels, depending on their shape and design (Buckland and Walpole, 1873) and woven from willow, Salix sp. These were fixed on the river bed or set in wooden-framed fishing weirs (Sjöberg, 2011). Woven baskets with throats were used in Britain from medieval times to the early 20th Century, but today all gear is of synthetic materials. Fyke nets, rigged with the mouth facing downstream and short leaders have been used, but are subject to becoming clogged with debris during autumn spates when most adult river lamprey migrate upstream in western Europe. Alternatively, river lamprey are caught in 'pots' fished in lines down the thalweg. This fishing method is also found in France, where specific pots for river lamprey are used by a few fishermen, although in most cases lampreys are a bycatch from other fisheries (Table 1).

Baskets are also traditionally used in Finland since the 15th Century (Tuomi-Nikula, 1981) and continue to be used in all the rivers where river lamprey are harvested (Kaski and Oikarinen 2011). The original baskets were made of willow shoots or twigs (osier basket), or of other similar flexible material (juniper, spruce; Sjöberg, 2013), but have been replaced by modern baskets made of plastic mesh. While baskets are used in the fast flowing parts of rivers, fyke nets are typically set in estuaries (Table 1). Baskets and pots were also commonly used in Sweden, with pots often used at weirs (Sjöberg, 2013). In Estonia lamprey fyke nets or cone traps are set in lines and are limited in terms of trap height and width (Table 1; Baikov et al., 2017; Sjöberg, 2013). In Latvia, river lamprey are caught primarily in fyke nets, trammel nets, and lamprey weirs. Lamprey weirs are also operated in shallow fishing areas with hard bottom substrate and relatively high current velocity. Such fishing grounds are located on the Salaca, Svetupe, and upper Venta rivers (Fig. 1; Abersons and Birzaks, 2014). Trammel nets are used only below Riga HES and Riga city during periods of water accumulation in the reservoir. In Lithuania fyke nets are used in the Curonian Lagoon and the Šventoji River, while baskets are used in the Nemunas River Delta (Table 1). As the tradition of wicker weaving is dying out, synthetic materials are increasingly used for cone traps. In Russia, before the development of the commercial fishery, river lamprey were often taken out of ice holes with different types of nets (e.g., scoops, buckets; Sabaneev, 1892). In addition to the generally accepted fishing gears described above, lamprey trapping based on underwater illumination was developed in the former USSR in the middle of the 20th Century. This method is based on the negative reaction to the light observed in lamprey. Powerful underwater lamps are equipped with metal shields that block the light on one side are placed on the riverbed in such a way that, with the exception of a narrow dark corridor in the middle, the entire stretch of the river is flooded with bright light. Lamprey migrating upstream to spawning sites go through the dark section of the river and enter traps set at the end of the resulting dark corridor (Rass, 1971).

Being a species that is commercially harvested in many countries, particularly in the Baltic region, river lamprey could benefit from a joint international management and conservation program. In fact, management actions implemented in several countries aim to reduce fishing mortality, so a coordinated effort could prove to be more cost-efficient by defining closure periods and/or no-take rivers.

The major factor regulating harvest of lamprey both in Finland and Sweden is land ownership. This has prevented any large sudden changes in fishing effort from taking place (i.e., number of fishermen). It has likely also suppressed "the tragedy of the commons" (Hardin, 1968). Fishermen occupy the same fishing sites with the same gears year after year, and they know their neighbor's fishing, share the same information base, and can set up additional fishing rules. This adds stability and engenders commitment to sustainable fishing through self-organization (Poteete et al., 2010).

However, the sustained market for lamprey along with depressed populations in the Bothnian Bay after the 1970s resulted in increased Finnish harvesting. Effective fyke nets became more common in lamprey fishing at the same time, which further intensified harvest. Since the 1990s, catches have further decreased and lamprey fishermen have aged. Both have contributed to the gradual decrease in harvesting (Kaski and Oikarinen, 2011), even more so in Sweden than in Finland (Sjöberg, 2011).

In Finland, a fishing closure in spring and early summer essentially prohibits fishing during the lamprey spawning season, but allows fishing during the entire spawning migration period. In Sweden, no such closures are enforced nationally. There are also no directed measures (e.g., quotas, extra closures) set for the Finnish and Swedish lamprey fishing on a national level. However,

Fig. 9. Tribal harvest of Pacific lamprey at Willamette Falls, Oregon City, Oregon, USA. Photo credit Jeremy Five Crows, Columbia Intertribal Fish Commission.

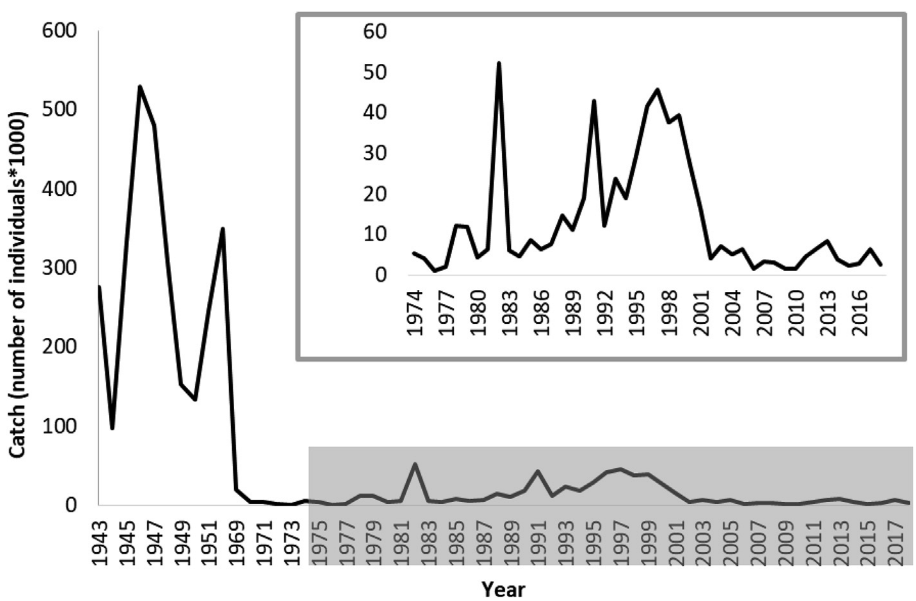



Fig. 10. Pacific lamprey harvest (number of individuals) at Willamette Falls between 1943 and 2018, Oregon City, Oregon, USA. Note inset has expanded scale for later years.

there is locally organized regulation (see above). Similarly, in Finland, there is river-to-river variation in fishing access and/or the amount and type of gear in use to increase escapement when abundance of upstream migrating lamprey is low (Hiltunen et al., 2013). For instance, attitudes towards fyke nets vary significantly, and in some rivers fyke nets are totally forbidden (Kaski and Oikarinen, 2011). In two Finnish rivers (i.e., Kalajoki and Perhonjoki rivers) exploitation rates of lamprey have been studied almost annually since the early 1980s (Aronsuu et al., 2019; Laitala, 2019; Vikström, 2018). In the Kalajoki River, fishing mortality in 1980–2009 averaged 50% and in Perhonjoki River ca. 44% (cf. Fig. 5). Similar exploitation rates were reported in the late 1970′s for the Pyhäjoki River, Finland (Valtonen, 1980). Tagging experiments indicated that fishing mortality decreased markedly during the 2010s in the River Perhonjoki. In 2002 and 2004, fishing mortality was estimated to be only 10% in the Kymijoki River, which drains to the Gulf of Finland. However, estimates of exploitation rates are largely lacking, especially in large rivers.

In the northern Baltic Sea, lamprey have been monitored using catch statistics, studying larval densities, and estimating abundance of upstream migrating adults and outmigrating juveniles via test fishing and tag-recapture. Monitoring has been focused on certain rivers and the analyses and interpretation of the data have been supplemented by some one-off studies required as mitigation for operation of hydropower dams (Aronsuu et al., 2019). Both the Finnish and the Swedish studies (e.g., Ojutkangas et al., 1995; Hiltunen et al., 2013; Aronsuu, 2015; Tuunainen et al., 1980; Valtonen, 1980; Aronsuu et al., 2019; Sjöberg, 2011) indicate that the decline in the lamprey catch and population size in the last century primarily arose from degradation of habitat necessary for the natural life cycle of river lamprey (Lucas et al., this issue). Larval densities have varied independently of escapement; that is, reproductive output has been mostly driven by factors other than the abundance of spawning stock (Aronsuu et al., 2019). Nevertheless, exploitation rates in many rivers are substantial, and regulation of fishing mortality should continue to be included amongst lamprey rehabilitation measures (Aronsuu, 2015, 2019).

In Lithuania, river lamprey catch limits are set by the Ministry of Environment every year with auctions for Individual Transferable Quotas in the Šventoji River (1.5 tonnes) and the Nemunas River Delta (2 tonnes). In the Šventoji River, fyke nets are used to catch lamprey, but in the Nemunas River only traditional willow baskets are allowed. In the Lithuanian part of the Curonian Lagoon the fishery is closed from January 1 to September 15. Presently, up to 220 Special Fishing Permits are issued annually in Lithuania. Daily or weekly permits are issued for 1–31 May or 1 June to 31 December, for a maximum allowed catch of 50 river lamprey per permit. Seniors and underage are not required to purchase a permit, but they are limited to a catch of 10 lamprey.

The amount of lamprey fishing gear in Latvia is limited to 571 fyke nets and 31 trammel nets. Fishery closures differ amongst rivers, with the shortest in the Daugava River (May 1 to July 31) and the longest (February 1 to July 31) in the Brasla, Gauja, Irba, Lielupe, Saka, Salaca, Svētupe, Užava and Venta rivers. All other rivers are closed to lamprey fishing from February 1 to October 31. More than 60 years ago, Latvia started an artificial reproduction and restocking program for river lamprey. Larvae were raised in the hatchery of the Bior Scientific Institute. In 2019, alone, two million larvae were released into the Daugava River. In 2015 the Latvian river lamprey obtained the status of ‘‘national treasure”, and the Carnikava lamprey became the first Latvian product to be awarded the PGI mark, i.e., a Protected Geographical Indication.

The Estonian lamprey fishery is essentially managed by imposing limits to the fishing effort. There is a maximum limit of 18,300 cone traps and 81 fyke nets. Up to 5000 cone traps can be set in the Narva River, with the remainder distributed amongst other rivers. The fishery closure extends from March 1 to July 1 (Armulik and Sirp, 2017).

Monitoring in Lithuania, Latvia and Estonia is carried out under the EU Habitat Directive (92/43/EEC) and largely targets status of river lamprey in the Natura 2000 network of protected areas. River lamprey monitoring is based on larval density estimates, and poor river lamprey status could lead to fishery closures. The intensity of monitoring varies between the countries; annually in Latvia but on an irregular basis in the rest of the region and mainly at Natura 2000 sites.

Management of the river lamprey stock in the Baltic states is likely affected by a high rate of illegal fishing. Increased poaching has been fuelled by high demand and increasing price. For example, in Latvia 2970 lamprey were captured in 2016 by illegal traps set in the Daugava River (Riekstiņš et al., 2018). Similarly, in 2014 the Estonian Environmental Inspectorate removed 17,483 illegal cone traps from the Narva River. In the next two years the number of illegal traps had decreased to 7378 and 900, respectively (Armulik and Sirp, 2017). In Lithuania, the scale of illegal fishing is not evaluated, but some catch is probably misreported. Although illegal, the tradition of handpicking spawning lamprey is still common and one can pick several hundred lamprey in one night. While how illegal catches compare to official statistics is unknown, failure to comply with the existing rules and gear limitations can make lamprey stock management based on catch data meaningless. It could also explain why legal catch as in Latvia has declined in recent years.

In Russia the river lamprey fishery is regulated by International, Federal and Regional laws. It occurs in the 26th and 32nd Subareas of the Convention Area of the International Council for the Exploration of the Sea (ICES) and the fishing restrictions mainly concerns the spring and summer periods. The ban on fishing is lifted on July 31 (June 30 in the Narva River). Catch without permission is punishable by law with a heavy fine for each adult lamprey caught during the legal fishing, and even higher penalties during fishing closures (Anonymous, 2020). In addition to restrictive measures, Russia is actively pursuing a policy of restoring the population of river lamprey via the annual release of artificially produced larvae. This restocking program, coordinated by the fishery authority (Glavrybvod), annually releases up to 4 million larvae. Several private companies financially contribute to this program as partial mitigation for their environmental impacts. To date there are no public results from this restocking program.

In Britain, where commercially fished river lamprey are sold as fishing bait, rather than eaten, control of the fishery has developed progressively. From 1995 until 2009 British lamprey were legally caught as by-catch in authorized eel fisheries. Lamprey were not recognized by national fisheries legislation, and their exploitation could not easily be regulated. This was a significant concern for the Yorkshire Ouse and Trent rivers fisheries, adjacent to the Natura 2000 Humber Estuary Special Area of Conservation. According to the EC Habitats and Species Directive, lamprey fishing should be regulated on a precautionary basis, yet the relevant authorities were unwilling to do so. The UK Marine and Coastal Access Act 2009 provided the necessary legal means for control, and after 2011 lamprey fisheries were strictly regulated. Masters et al. (2006) estimated that the exploitation rate in the 2003–2004 season was 9.9%, adjusted to 12% for tag loss. Fishery managers allowed only existing fishermen to apply for licenses, limited the number of pots they could set and applied a total quota of 1044 kg (ca. 13,050 lamprey) for a 6 week open season on the Ouse, with that for the Trent set at 20% of the Ouse value based on observed CPUE differences between the rivers. Noble et al. (2013) obtained a river lamprey exploitation rate of 2.01% for the commercial fishing season on the Ouse using similar methodology to Masters et al. (2006), estimating that the run size in fishing season 2011–12 was ca. 655 000 lamprey. Several indices showed that Ouse CPUE from 2011 to 2016 was generally lower than during a comparable period (1 November to 10 December) in 2000–2008. On this basis, the fishery was suspended for 2 years (2017–2018) to aid recovery. Fishers were paid to gather CPUE data for monitoring, with captured lamprey transported upstream of the first two river barriers. In 2018–2019 further exploitation rate studies occurred, together with telemetry studies to determine the impact of the fishery relative to other factors (e.g., fish passage constraints at barriers). Fishing at a lower quota recommenced in 2019. The fishery has caused local debate partly because water abstracting industries have been required to reduce lamprey and eel impingement at great cost while lamprey fishing has continued. However, the fishery also provides one of the few sources of relative abundance data for the adult lamprey population without substantial costs to regulatory agencies.

Lamprey continue to be used as bait in spite of their conservation status. Although the Pike Anglers Club of Great Britain has emphasized the endangered status of European eel (PAC, 2019), they make no mention of the need to conserve lamprey. Luckily, the use of artificial lures for pike remains the preferred angling method outside of the UK. Engaging stakeholders such as anglers in fish and habitat conservation is needed (Danylchuk and Cooke, 2010).

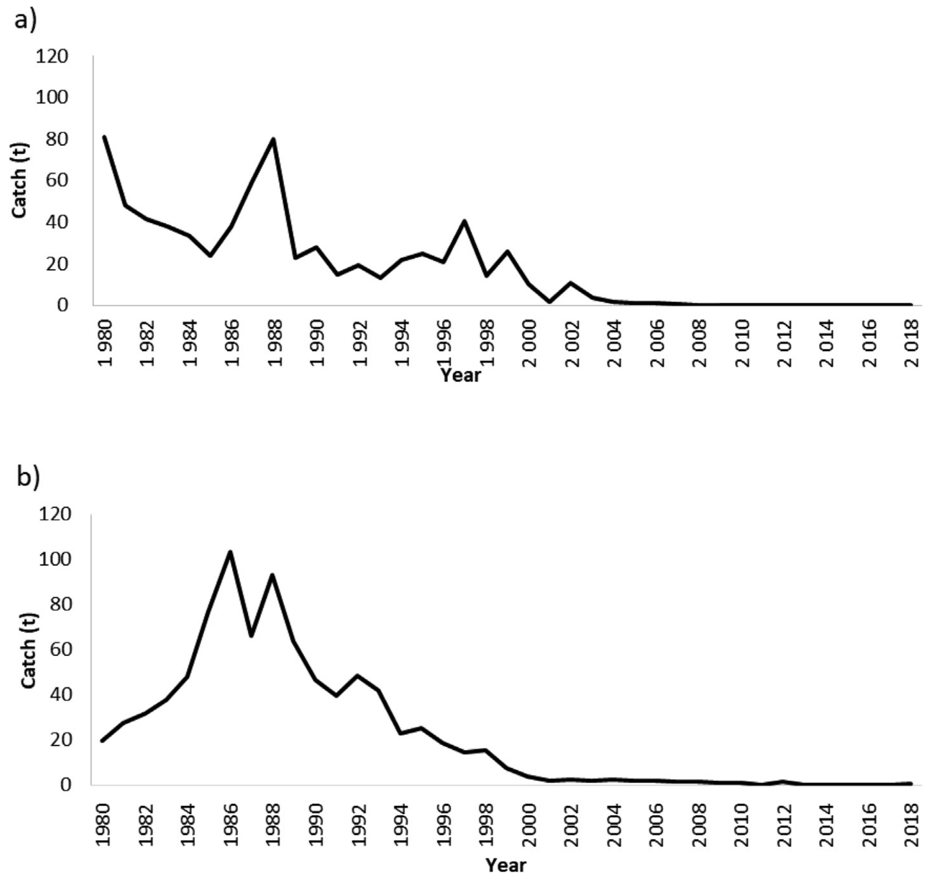



**Fig. 11.** Arctic Lamprey harvest (t) in Ishikari River Basin, Hokkaido, Japan: a) Shirivetsu River; b) Ishikari River, from 1980 to 2018. (Source: Salmon and Freshwater Fisheries Research Institute, HRO).

**Fig. 12.** Trap used to catch Arctic lamprey in the Ishikari River, Ebetsu City, Hokkaido, Japan.

In France, river lamprey exploitation is regulated by the same mechanism as described for sea lamprey earlier. In the Netherlands, where bycatch of river lamprey in eel fyke nets had been sold to the UK as fishing bait, changes in national regulations now preclude this and require their return to rivers alive.

## Pacific lamprey

Pacific lamprey is an anadromous species reaching ca. 80 cm in length and 510 g in weight, which exhibits a very broad distribution, ranging from Baja California in the eastern Pacific Ocean, northward to the Bering and Chukchi seas, and westward into Russia and Japan (Orlov et al., 2008; Renaud, 2011).

Pacific lamprey (referred to as "eels") are an important cultural resource for Native Americans in the northwestern United States, with traditional fisheries occurring from time immemorial (CRITFC, 1994). Many tribes from northern California, Oregon, Washington and British Columbia value Pacific lamprey as a traditional food source. For indigenous peoples of the mid-Columbia River Plateau, Pacific lamprey is of religious significance and is considered a "first food" (Close et al., 2002). Native Americans also rely on lamprey oil for medicinal purposes: it is applied to the body for traditional purification sweat baths, used as a hair conditioner, and to treat earaches (Close et al., 2002).

Native Americans typically harvest adult Pacific lamprey by hand from waterfalls (Willamette Falls, Fig. 9) or by dipnet, jigging with a long pole, or using traps (Klamath River) (Table 1). They are typically prepared by drying or roasting and remain a critical component of tribal celebrations and ceremonies (Close et al., 2002).

While tribal harvest in the Columbia River basin predates catch record keeping, significant commercial harvest has been documented since the early 1900s (Close et al., 2002). Lamprey were harvested in large numbers for fish feed and by 1913 the catch was approximately 24.5 tonnes (Clanton, 1913). High levels of exploitation occurred during the 1940s and 50s (Fig. 10), with over 740 tonnes harvested between 1943 and 1949 for use in livestock feed, oil and fishmeal (Close et al., 2002). Lamprey were also used for scientific teaching/research and for food (e.g., 1816 kg were exported to Europe as a food fish in 1994, Close et al., 2002). Commercial harvest of Pacific lamprey in Oregon was prohibited in 2001 when the catch declined to less than 13,000 individuals (Close et al., 2009). This occurred at a time when traditional knowledge from tribal elders clearly indicated a long term population decline in the upper Columbia River basin (Close et al., 2004).

Tribal harvest occurs along the US Pacific coast from the Columbia River south to the Klamath River (Fig. 1b; Petersen, 2006). Tribal elders maintain that lamprey populations in the Klamath River began to decline significantly about 40 years ago. At that time, seasonal tribal catches were 1000–1500 lamprey annually; but, the tribal catch has dwindled to double digits (Larson and Belchik, 1998; Petersen, 2006). Coastwide lamprey declines are attributed to passage barriers, historical overharvest, and habitat degradation (Petersen, 2006).

Pacific lamprey today are primarily harvested by Native Americans during spawning migrations in streams and rivers of Washington, Oregon and Northern California (Pacific Northwest of the USA). Catches commonly occur at traditional fishing areas near waterfalls where lamprey congregate. Currently, tribal fishing is restricted to a few sites in the Columbia River basin (e.g., Willamette Falls, Schearers Falls), several small coastal rivers (e.g., Coquille River, Oregon) and the Klamath River basin.

Effective management actions for anadromous fish depend on the knowledge of the target species biology, population structure and migratory dynamic, namely during the marine phase of their life cycle (Mateus et al., this issue). For the Pacific lamprey, movement patterns in the Pacific Ocean and stock structure throughout their range are poorly understood. Studies indicate gene flow across large geographic areas (Goodman et al., 2008; Spice et al., 2012), and Pacific lamprey may transit thousands of kilometres from ocean feeding areas to freshwater spawning sites. This is exemplified by the detection of a single adult tagged in the Bering Sea and subsequently detected in the Columbia River basin (Murauskas et al., 2019). Hence, fisheries for Pacific lamprey could have impacts on recruitment at the opposite end of their range.

In the northwestern United States, lamprey are harvested by indigenous peoples at limited sites under tribal treaty rights. Reductions in lamprey abundance have reduced tribal fishing areas and the numbers collected. Undoubtedly, high commercial exploitation levels in the early part of the 1900s contributed to declines in Pacific lamprey abundance. However, these large harvests also coincided with targeted extirpations, construction of dams that blocked passage, and habitat loss (Close et al., 2009). Demographic fluctuations in the abundance of common hosts in the marine environment could also help explain the observed decline in lamprey abundance (Murauskas et al., 2013, 2016).

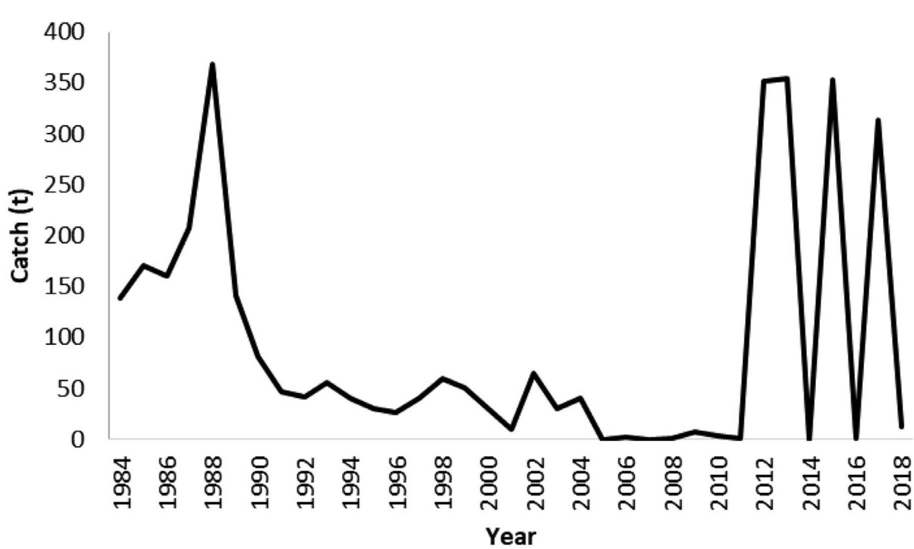



**Fig. 13.** Arctic lamprey catches (t) in Amur River (Russia), from 1984 to 2018.

Visual counts of adult lamprey passing mainstem dams in the Columbia River provide an index of abundance (Clabough et al., 2012). The lamprey available to tribal resource agencies for research and restoration is prescribed as a given percentage of this index, which is negotiated amongst the treaty tribes and codified in a tribal plan for Pacific lamprey restoration (CRITFC, 2011). Tribal harvest is managed via quotas and/or seasonal closures to minimize impacts to recovering populations. For example, tribal harvest at Willamette Falls was estimated at 4.4%–7.3% of total adult escapement estimates (Baker and Graham, 2011).

In Japan, *E. trindentatus* is known to occur around the Pacific Coastal area, especially in in the rivers of the Tochigi Prefecture (Fukutomi et al., 2002; Yamazaki et al., 2005). This species is very rare and considered data deficient by the Red Data Book of Japan (Japan Ministry of the Environment, 2003). Hence, its exploitation has not been historically established. Furthermore, the population seems to have been declining in the last decade (Tochigi Nakagawa Aquatic Park, pers. com., 2020). The Tochigi Natural Park used to conduct field surveys and had an exhibition showcasing live Pacific lamprey until 2016; but since 2017, the exhibition was closed due to the inability to collect any Pacific lamprey from the rivers in Tochigi (Hiroaki Arakawa and Tochigi Nakagawa Aquatic Park, pers. com., 2020).

In Russia, despite the increasing abundance of Pacific lamprey in coastal/oceanic waters, the Bering Sea and Sea of Okhotsk (Orlov and Baitaliuk, 2016), there is little information of its migration into fresh water for reproduction in Russian rivers, with evidence suggesting they might feed in the Bering Sea and migrate to spawn in Canada and US rivers (Murauskas et al., 2019). Therefore, as in Japan, there is no history of a fishery associated with this species in Russian rivers.

## Arctic lamprey

The Arctic lamprey is an anadromous medium-sized species (ca. 63 cm in length), widespread from the Siberian coast to the Anderson River in Canada in the Arctic basin and from the Bering Sea south to Japan and Korea in the northwest Pacific. It also occurs in the Arctic, White and Barents Sea basins of Russia and Norway (Renaud, 2011; Orlov et al., 2014; Orlov and Baitaliuk, 2016).

Reports from the last quarter of the 19th Century mention that upstream migrants were harvested in large quantities by native people in parts of the Yukon River (e.g., Russian Mission, Anvik) (Fig. 1b) (Turner, 1886). The oil from Arctic lamprey was used for human consumption or as fuel for lamps (Renaud, 2011). According to Renaud (2011), there was some will to begin a commercial fishery in the beginning of the 21st Century that could supply the Asian market in the USA and in foreign countries, with a 20 tonnes quota established in 2003. In November, after 3 h, more than half of that quantity was harvested near Saint-Mary (Horne-Brine, 2007). Allegedly part of the catch is exported to Portugal, but in fact there is no evidence that any Arctic lamprey are sold in Portugal so far (P.R. Almeida, pers. com., 2020).

In Japan, Arctic lamprey is captured throughout Hokkaido Island to the middle of Japan and along the Sea of Japan (Kataoka et al., 1980; Murano et al., 2008; Arakawa et al., 2018). In the past, Arctic lamprey supported important commercial fisheries in most large rivers draining to the Sea of Japan. Due to its rich content of Vitamin A (MEXT, 2015), Arctic lamprey has been used as a Chinese medicine for preventing night blindness. An ancient Japanese encyclopedia (Wakansanzuie) published in 1712, described lamprey consumption. Lamprey is known as an important food resource for rural residents (Satoyama), being captured both by recreational or self-subsistence fisheries.

There is a diversity of regional lamprey dishes. Restaurants in Ebetsu City, Hokkaido, offer grilled, fried and raw Arctic lamprey caught in the Ishikari River. Lamprey is also eaten simmered and in a soup seasoned with soy sauce or soybean paste (miso). Arctic lamprey are also preserved dried and later consumed grilled.

The Ishikari River, located in central Hokkaido, is the second largest drainage area in Japan (14,430 km2) and the main fishing area for Arctic Lamprey (Fig. 1b). Native Ainu tribes lived a life of hunting and fishing salmonids and lamprey until the 1868 government accelerated development of land for agricultural and urban uses. The lamprey harvest in the Ishikari and Shiribetu rivers (1640 km2) in Western Hokkaido peaked at 80–100 tonnes in the 1980s, but declined in the 1990s and had essentially disappeared by 2000 (Salmon and Freshwater Fisheries Research Institute, HRO unpublished data, Fig. 11). The annual lamprey festival in Ebetsu along the Ishikari River died out due to the collapse of harvest after 2001. On the main island of Japan, the Mogami River (Yamagata Prefecture), the Agano River and the Shinano River (Niigata Prefecture) are famous for lamprey catches (Fig. 1b). The Machino River on Noto Peninsula (Ishikawa Prefecture) represents the southern limit of traditional lamprey fishing. It was estimated that the quantity of Arctic lamprey harvested in the 2010s decreased to 1–10% of the past catches (Arakawa et al., 2018; Arakawa and Yanai, in press).

Historically a variety of Japanese fishing methods have been developed in accordance with season, river size and aquatic environment (Table 1, Arakawa and Yanai, in press). One of the methods uses fyke nets and cylindrical basket traps which are made from metal and fiber or plant material such as bamboo (Fig. 12). This technique is carried out in the mainstem of large rivers (e.g., Ishikari, Mogami, Shinano, Agano rivers) during an early winter and spring season (Fig. 1b). A second method is gaffing lamprey using a hook attached at the tip of a long stick or grabbing single lamprey concentrated downstream from barriers. The fishing season is from winter to spring and catches increase at night and with a new moon, especially when the water level rises. This fishing method is mainly carried out at weirs in the middle reach of small and medium-sized rivers (e.g., Aka, Miomote, Shinano, Machino rivers). A third method captures lamprey on their spawning bed using a hook, harpoon, or by hand. This fishing method is carried out in the upper reach of tributaries from spring to early summer.

In the European part of Russia, Arctic lamprey are captured in the Arkhangelskaya Oblast where harvest is permitted in December (Fig. 1b). The first commercial records are from the 18th Century. and local fisheries are described in the historical notes of the 1772 expedition by the academic Ivan Lepyokhin (Fomin, 1805). The local community used lamprey both fresh (grilled or baked) and marinated. Elena Molokhovets (1861) provides a recipe for roasted lamprey in her popular book "A Gift to Young Housewives", which was written for the middle class and aristocrats.

In the early 20th Century, a commercial fishery developed in Northern Dvina and a plant for processing lamprey was installed (Kozmin, 2011). However, the resulting product had no value to the local market, as native people took lamprey for snakes (Ivanova-Berg and Manteuffel, 1949). In Siberia, lamprey never had any fishery value, although larvae were used as a fish bait. In the easternmost part of Russia, local folks (i.e., the Nanais) dried lamprey to make candles.

The main fishing areas for Arctic lamprey in the European part of Russia are in the Onega, Mezen (and its tributaries Irva, Bolshoi Subbach, Maly Subbach, Elva, etc.), Vashka, Northern Dvina, Vychegda, Vyg, and Nes river basins (Fig. 1b; Berg, 1948; Ostroumov, 1954; Solovkina, 1954; Martynov, 2002; Kozmin, 2011). In these rivers, lamprey fishing coincides with harvest of burbot (*Lota lota* (L.)). In the Far East, the lamprey fishery is still undeveloped, but it is present in the Amur (and its tributaries), the Suchan and other eastern rivers (Fig. 1b) (Anonymous, 2013). The Amur River basin is one of the largest fishing areas in Russia and the estimated lamprey stock is ca. 13% of all the commercial freshwater fishes. The lamprey fishery is concentrated 750–950 km upstream from the Amur River mouth (Anonymous, 2013, 2019). In the late 1980s, the lamprey catch exceeded 100 tonnes, but since 1990, it has decreased significantly along with a decline in consumer demand. In 2005, fishing in the Amur River was banned due to an accident at a chemical plant in China. Later, despite the good condition of the stock, lamprey were caught in insignificant quantities and only for scientific research purposes. The lamprey fishery was resumed in 2012–2013 (Fig. 13) (Anonymous, 2013, 2019). The decline of the lamprey harvest after 1990 was due to a decrease in fishing effort: 340 traps before 1990, 62 traps in 1990–2004, and 11 traps in 2005. In 2012–2013 the number of traps increased to 390–395 (Anonymous, 2013).

Bottom minnow traps (Krysanov, 2000; Makhrov et al., 2013), set to catch Arctic lamprey, are fixed under ice during the upstream migration of lamprey at the end of November to January in the Northern Dvina and Mezen rivers (Novikov, 1964). Only in the Onega River does fishing begin before freeze up. Catches come from narrow stretches of the river (especially in the Mezen River), and mass fishing occurs in just 10–25 days. Two further types of traps are used: meshed ("ryuzhi") in the Mezen River and lower reaches of the Northern Dvina, and wooden baskets made of spikes and twigs used in the Onega River and the upper part of the Northern Dvina (Table 1). Spike traps are also set in rows across the river in combination with barbed fences. In winter, lamprey are also caught in ice holes with nets or simple wooden hooks or sickles (Manteuffel, 1945; Jacobson, 1914; Krysanov, 2000).

Actions addressing the management of the Arctic lamprey have followed distinct paths across the species' distribution range. With the decline of the species in Japan, there was an increased motivation for conservation of populations and traditional culture. The Ishikari and Sorachi Subprefectural Bureau worked on an Arctic lamprey conservation project for three years (2004–2006). This project targeted fishermen and workshops were held on artificial propagation techniques. The ecological role of ammocoetes (Shirakawa et al., 2009, Shirakawa et al., 2013) and habitats critical to spawning were identified (Shirakawa et al., 2011). Large side channels were artificially created to provide habitat for larvae by the Hokkaido Development Bureau and a supplemental guide book explaining the lamprey biology was published as outreach to the community (Murano et al., 2008). However, there are still few efforts to revive and conserve Arctic lamprey throughout Japan, despite its cultural importance and awareness of population declines.

In contrast, Arctic lamprey in Russia has never been a management focus. However, in Khabarovsk Krai and Jewish Autonomous Region (EAO), where harvest is regulated by federal (Ministry of Agriculture) and regional laws, there are regulations and orders that specify annual Total Allowable Catch (TAC) allocation (Khabarovsk NIRO), prohibited catch locations, gear size and technical specifications, temporal closures and size limits. Since 2011 the TAC for these two regions was constant, in the Amur River basin, the TAC for Khabarovsk Krai is 400 tonnes and for the EAO is 100 tonnes (Anonymous, 2019).

An analysis of Russian fishing reports shows that the actual Arctic lamprey catch is lower than the allowable catch in recent years. In the Amur River, tagging results showed that the long-term average sub-adult stock is relatively stable at close to 10 million specimens. With an average body weight close to 100 g, total biomass is about 1000 tonnes. According to the data provided in the justification of the TAC for the Amur region (Anonymous, 2019), lamprey is identified as a species that preys upon chum salmon (*Oncorhynchus keta*; Walbaum, 1792) fry during trophic outmigration and, consequently, it is recommended that at least half of the upstream migrating adults be harvested (Birman, 1950; Anonymous, 2019).

The influence of Illegal, Unreported and Unregulated (IUU) lamprey fishing in Russia is unknown. Even though the fine for each illegally caught lamprey is high, this kind of activity is widespread. Handmade traps are often left in rivers, and lamprey caught in them die without reproducing.

**Caspian lamprey**

The Caspian lamprey is an anadromous species endemic to the Caspian Sea, with a length ranging from 19 to 55 cm and a maximum weight of ca. 206 g (Renaud, 2011). Previously, Caspian lamprey were dried and used as candles or for their oil, and harvested for human consumption (Kottelat and Freyhof, 2007; Renaud, 2011). Caspian lamprey meat was considered to have excellent taste and a high-fat content at the beginning of migration (Kazancheev, 1956). Lamprey were used for food and for lighting by the non-Muslim population of the Russian Caucasus, whereas Muslims only used this resource for non-gastronomic purposes, such as candle manufacture.

This species has had particular cultural and socioeconomic importance as a fishery both in Volga River, Russia and in the Kura River, Azerbeijan (Fig. 1b; Nazari et al., 2017), with records of substantial catches in the late 19th – early 20th Century (Berg, 1948). The Caspian lamprey is also caught in other rivers in the region, although not nearly as much, and its decline has been range wide. In the southeastern Caspian region, Caspian lamprey has historically been used by the Turkmen for its medicinal properties (Nazari et al., 2017).

In Iran, and other countries of Muslim majority, lamprey is not consumed due to religious reasons (considered "haram") and thus it is not commercially harvested. Nevertheless, it has been captured and used for treating health problems and also for human consumption, whether smoked or in brine, for instance in the Gorganrud River (Fig. 1) (Coad, 2016; Nazari et al., 2017; Shirood Mirzaie et al., 2017).

The Russian population of the Caspian basin harvested this species for about 300 years, until the mid-20th Century, when the construction of instream barriers blocked their spawning migration routes. Presently, this species has lost its socioeconomic importance. The Caspian lamprey directly or indirectly has even affected the migration of people from central Europe to Russia (i.e., Sarepta settlement), due to seasonal labour migrations in the Volga region. The ability to roast lamprey was highly valued, and the masters of this business travelled to the Volga region as skilled workers for lamprey frying (Ferschel and Tuvi, 2010).

In the first decades of the 18th century, fisheries were actively developing in the Simbirsk-Samara Territory, through which the Volga, Sura, Sviyaga, Barysh, Alatyr, Usa, Samara rivers flowed (Fig. 1b). Although sturgeons and other fish were of greater value, the Caspian lamprey was also harvested to obtain fat. The community leaders of Sarepta in the mid-18th Century tried to develop a commercial fishery on the Volga, with high hopes for profit from the extraction of "red" fish (i.e., salmon and sturgeon) and black caviar for the Russian market. Fishing in Sarepta was initially conducted on the Volga, Sarp and some lakes. Later, the community hired numerous groups of local Volga fishermen for fishing in their waters. In winter, local people conducted ice fishing for lamprey, burbot and whitefish *Coregonus* sp. (i.e., all fish species except salmon and sturgeon; Pallas, 1788).

In the 19th Century catches of "red" fish which had previously been abundant in Sarepta-Chernoyarsk waters markedly decreased and so cartels increasingly turned to fewer valuable fish species, such as the Caspian lamprey. Lamprey was caught in the summer to obtain oil and in the winter it was salted and delivered to the markets (e.g., Moscow, Riga, Nizhny Novgorod, Smolensk, Kyiv) (Minh, 1902).

In the late 19th and early 20th centuries, lamprey fisheries on the Volga River peaked, with a total catch in the lower reaches of 17–33 million specimens in the 1910s (Berg, 1948). Probably, even then, the harvesting in such quantities was a serious burden to the population. For instance, in 1910 16.9 million specimens were caught in the lower reaches of the Volga River, and only 17 thousand were caught in the Saratov region, in the middle Volga (Kalaida and Govorkina, 2017).

The industrial growth of the former USSR promoted the construction of cascades of hydroelectric dams and reservoirs on the Volga River to meet electricity needs. Simultaneously, there was an expansion of water-intensive crops and general impoundment for irrigation. These habitat alterations had a negative effect on the population of Caspian lamprey. It was missing from the fish fauna in the first years after the closure of the Volga dams along with a dozen other anadromous species of fish (Poddubny, 1971; Sharonov, 1962; Bogutskaya et al., 2013).

In the Kura River, from 1891 to 1935 (5-year cumulative reporting intervals), the minimum catch was reported in the 1891–1895 period when only 11,000 lamprey were caught, whereas in 1911–1915 captures peaked and the reported catch was of 612,000 individuals. After 1935, 213,000 were caught in 1936 alone and in 1937 the reported catch was of 304,000 lamprey (Berg, 1948). Nowadays this species is no longer considered commercially important, due to the severe stock reduction that took place after water regulation projects were established in both the Volga and Kura rivers (Nazari et al., 2017).

Currently, the species is listed in the Red Book of the Russian Federation. In small quantities, it is found in the lower reaches of the Volga River, as well as in the Ural, Terek, and Kura rivers (Fig. 1b). It spawns during the winter and reaches the Chechen Republic (Abdusamadov et al., 2011). In Iran (Fig. 1b; Gorgan, Babol and Sardab rivers), the number of Caspian lamprey is relatively high. During the spawning run up to several hundred kilograms of Caspian lamprey can be caught within an hour (Coad, 2015).

Caspian lamprey were caught using different methods, such as the wicker net (tensioned on wooden hoops), which consists of a cone-shaped trap with wings (net walls) on the sides, used both by fisherman and anglers. Wicker traps were made of thin twigs of willow and usually installed near the shore. Lamprey were also caught in ice holes during winter by local people using their hands and nets (Table 1; Pallas 1788).

To the best of our knowledge, there are no specific management actions focusing on the harvest of the Caspian lamprey.

## Korean lamprey

Korean lamprey is a small freshwater species (ca. 29 cm) mainly distributed in the Yalu River and other mountain rivers in northeast China, North Korea and the Russian Far East (Renaud, 2011). This species was very abundant in the Hunjiang River, a tributary of the Yalu River (Fig. 1; Ma and Yu, 1959).

In the past, in China, Korean lamprey was regarded as harmful because it preyed on other fish (Ma and Yu, 1959). Its economic value was considered to be very low and it was even mistakenly thought to be toxic (Yang et al, 2017). People often saw them while fishing in rivers and streams. Since the 1980s, the economic value of Korean lamprey has increased in northeast China (Huang and Yang, 2009). People have been paying more attention to their edibility and, especially, their medicinal uses (Yang et al., 2017). With harvest increases came a decline in lamprey abundance, so that this important natural resource is now seriously endangered (Huang and Yang, 2009). Most likely due to its low productivity, this species is not presently exposed to major harvesting.

Fishermen in northeast China targeted mainly the spawning population of Korean lamprey. Traditional fishing involved setting a Yu Zhu net, an ingenious trap, which takes advantage of the local hydrological characteristics and the behavior of Korean lamprey (Table 1). The blocking net has the shape of a bow arc and two ends are curled, forming a trapping mechanism. The length of the net varies from tens to thousands of meters, and its height does not exceed the maximum water depth during periodic floods caused by heavy precipitation. During the period of rising water, adult lamprey invade the extensive floodplain, taking advantage of low flow conditions in this area. Fishermen recognize this behavior and place their nets blocking the connection between the floodplain and the river mainstem, catching lamprey that are returning to the river with the falling water.

In China the main threats to Korean lamprey populations are overfishing, destruction of habitat (e.g., dam construction; water pollution), and lack of management and awareness. Among the three species of lampreys occurring in China, Korean lamprey has the highest commercial value, and it is a good candidate for aquaculture (although there are currently no farms dedicated to this species). In view of the decreasing abundance of Korean lamprey, it is urgent to stop this decline and establish a sustainable fishery. This could be achieved through the implementation of a closed fishing period, preventing illegal fishing, improving knowledge regarding artificial reproduction and restocking techniques, revising local laws and regulations for species protection, and increasing public awareness to establish the concept of sustainable fishery production.

To protect lampreys in China, Arctic lamprey (*L. camtschaticum*) and Far Eastern brook lamprey (*Lethenteron reissneri;* Dybowski 1869) have been listed in the "China Red Data Book of Endangered Animals: Pisces" (Le and Chen, 1998) and "China species Red List" as Vulnerable (VU; Wang and Xie, 2004). Likewise, Korean lamprey should be added to these lists. At present, Liaoning Province and Jilin Province have identified Korean lamprey as key amongst aquatic wildlife for protection. In addition, Jilin Province has established the Tonghua Hani River National Aquatic Germplasm Reserve, a 458.6 ha area that is protected from April 1 to July 31 every year. The reserve is located in the Erdaojiang District, Tonghua City, Jilin Province, in the southwest Changbai Mountains, and includes the Taoyuan Reservoir and Hani River which is the first tributary to the Hunjiang River. Korean lamprey is among the protected species.

## Pouched lamprey

The pouched lamprey is one of the largest anadromous species in the southern hemisphere (ca. 57 cm), with a wide southern temperate distribution inhabiting southwestern and south-eastern Australia, Tasmania, New Zealand, Chile, Argentina and South Georgia Island (Renaud, 2011). Recent evidence has reclassified some populations along the south-east coast of South America as *Geotria macrostoma* (Burmeister, 1868) ( Riva-Rossi et al., 2020).

In New Zealand pouched lamprey are commonly known as "piharau" and "kanakana" in the North Island/Te Ika a Maui and South Island/Te Waipounamu, respectively. However, this species is also known by a variety of other names, including "korokoro", "pia", "pipiharau", "ute" and "waituere" (Best, 1929; Strickland, 1990). "Piharau"/"Kanakana" are an important taonga (treasured) species to a number of Māori iwi (tribes), hapū (sub tribes) and whānau (family) groups and its fishery has a high cultural importance. Customary harvesting occurs in a number of different locations in both the North Island/Te Ika a Maui and South Island/Te Wai Pounamu of New Zealand/Aotearoa. The harvest occurs during the adult spawning migration and lamprey flesh is a highly desirable delicacy that is considered to have health benefits (Kitson, 2012). Harvesting tends to focus on adults soon after they enter freshwater. After this time they turn a dull brown, males develop the distinctive gular pouch, and they are considered unappealing as food (Best, 1929).

It is thought that only a few non-Māori undertake recreational harvest, but there is no information on actual levels of this activity. There is some bycatch of "piharau"/"kanakana" during the popular spring harvest of whitebait (juveniles of five migratory galaxiid species). Some whitebaiters dislike "piharau"/"kanakana" as they are believed to interfere with their target species and at times these fish can be killed. The level of this bycatch is unknown.

This fish and fishery are important to iwi who harvest them, and contribute to their cultural identity, cohesion and as a vehicle for intergenerational knowledge transfer (Kitson, 2012). The customary association of Māori groups with this species has been recognised in contemporary legislation via treaty settlements and customary management mechanisms. No commercial fishery for lamprey exists in New Zealand/Aotearoa, however, historically there were some small-scale attempts in Southland (Jane Kitson and Stevie-Rae Blair, unpublished data).

There is little empirical data on temporal trends in this fishery and the species is not commonly targeted or captured in standard fish surveys in New Zealand. Historical accounts do demonstrate that this fish historically ascended rivers in great numbers. This is illustrated by the following quote:

> *"When i was at hokanu (Mataura River, Shland). In 1858 I had a stockman called George, a Sussex man,*
> *who came to the house one afternoon with a face as white as a sheet and swearing he had seen an eel at least a mile long at the Longford (now Gore). I got on my horse and went with him, and when I saw the phenomenon I was not surprised at his statement for I saw a column of kanakana more than a mile long, swimming in a round mass exactly like a large eel, so beautifully were they keeping a circular shape." (N. Chalmers quoted in* Beattie, 1994*).*

Most "piharau"/"kanakana" fishers have accounts of extremely large migration runs consisting of several thousand fish, many of which leave the river and cross land to surmount obstacles, blocking drains and crossing roads (Michael Bashford, pers. com., 2020), and climbing over sleeping fishers camping by the river (Peter Stockman, pers. com., 2020). Nowadays, migration runs and subsequent catches have declined and in the North Island some harvesters struggle to reach double digits across a season.

However, concerns over declining abundance and continuing threats to the fishery have resulted in management and research projects by different Māori groups on their respective rivers. Some have conducted monitoring of their catch over a number of years, however, this data is not published. Fisheries have been recorded in the North Island on the Mōkau, Waitotara, Patea, Waitara, Whanganui, Waipa and Ohinemuri rivers (Fig. 1b). In the South Island, harvests occurred across coastal Canterbury (including Ōrari, Ōpihi, Waihao, Temuka and Ohapi rivers and perhaps Waimakariri River), and in Otago and Southland on the Mataura, Clutha/Mata-Au, the upper Taieri, Catlins River, Waikawa, Silverstream, Pomahaka and tributaries of the Waiau River (Fig. 1b; McDowall, 1990, 2011; Todd, 1992; Anderson, 1998).

There are a variety of different methods to harvest "piharau"/"kanakana" in New Zealand, which vary depending on harvester preference, resources available (e.g., Bracken fern, *Pteridium aquilinum*) and river conditions. Harvesting is guided by site-specific "mātauranga" Māori (Māori knowledge), river flows, moon phases, astronomy, other environmental indicators (tohu), customary "lore"/"tikanga" Māori and principles of "kaitiakitanga" (the inherited responsibility to ensure sustainability of resources for the next generation; Table 1). Methods include, hand collection from rock outcrops or waterfalls (Downes, 1918; Beattie, 1920; McDowall, 1990; Anderson, 1998; Tipene and Jellyman, 2002; Vincent Leigh, pers. com., 2020); using long sticks with hooks at the end to pull "piharau"/"kanakana" out of holes in the river banks and rock crevices (Hall-Jones, 1992; Tipene and Jellyman, 2002; Duncan Ryan and Keith Bradshaw, personal communication.); pulling by hand out of holes in river banks (Shona Fordyce, pers. com., 2020; Jane Davis, pers. com., 2020); using hinaki nets or fyke nets in the river to intercept a spawning run (McDowall, 1990; Kelso, 1996; Vincent and Aaron Leith, personal communication); capture at "Whakaparu piharau" weirs made of stones with gaps in them and ferns placed underneath and behind them (Best, 1934; McDowall, 1990; Hayes et al., 1992; Kelso, 1996); "Whakarau", "whakapua", "taruke" and "pae" traps made of mats or bundles of bracken ferns to take advantage of refuge-seeking behaviour (Downes, 1918; Best, 1934; McDowall, 1990); and "Utu piharau"/"pā kanakana" wooden weirs built during low flows in summer and autumn. The weirs extend from the riverbank straight across the river for a set distance. Nets and lamprey pots are then anchored between vertical slots in the weir and face upstream. As lamprey migrate in the river margins to avoid swift flows, they find their pathway blocked and swim along the front of the weir to find passage upstream. Faster water velocities through the slots in the weir sweep lamprey downstream into the pots as they try to swim through the openings (Downes, 1918; Beattie, 1920; Best, 1924, 1929, 1934, 1941; Kelso, 1996; Anderson, 1998; Potaka, 2016).

The "piharau/kanakana" fishery is currently for customary or recreational harvest only, with no provision for a commercial fishery. The Ngāi Tahu Claims Settlement Act 1998 prohibits the commercial harvest within its tribal area (approximately 91% of the area of the South Island/Te Wai Pounamu). In the North Island, the Ngāti Ruanui and Ngāti Mutunga Treaty settlements specifically prohibit the commercial harvest of lamprey within their Protocol areas (parts of the Taranaki region) unless the Minister can demonstrate a commercial harvest is sustainable. There are also recreational regulations that limit the daily catch of "piharau"/"kanakana" to 30 in Southern and Fiordland areas.

Southland presently contains the most abundant "piharau"/"kanakana" populations in New Zealand and has been a focus of management actions and research. Two "mātaitai" (reserves) that encompass significant "kanakana" customary fisheries (Mataura and Waikawa/Tumu Toka) were put in place. Bylaws for the Mataura River Mātaitai Reserve prohibit the taking of "kanakana" without customary authorisation from the reserve's "tangata tiaki"/"kaitiaki" (those nominated from the local Māori community to be the managers and decision makers).

Other management considerations include maintenance of safe conditions for harvesters (i.e., free of toxicants, contaminants, or slippery conditions), provision of site access and abundant, healthy kanakana, and, perhaps most importantly, the intergenerational transfer of traditional knowledge. Low abundance or condition of "kanakana" populations has been a concern. Since 2011, the Lamprey Reddening Syndrome affecting migratory adults has rendered these fish inedible by most harvesters (Kitson, 2012; Brosnahan et al., 2018).

Site access is generally via "whakapapa" (genealogical) rights, however, access to sites can be impacted by conservation legislation and private or changing ownership. Managed flow regimes and abstractions can impact sites within rivers. Preferred fishing methods are impacted if bracken fern is not present. In the 1880s "utu piharau" (weirs) were removed by European settlers for navigation reasons on the Whanganui River. The Crown acknowledged and provided an apology for this removal in Te Awa Tupua (Whanganui River Claims Settlement) Act 2017.

Intergenerational knowledge transfer of the "mātauranga" Māori around the species and harvesting methods is crucial to the survival of this customary practice. The above factors can all impact on this transfer and some Māori communities are actively working to revitalise customary fishing methodologies. For example, on the Whanganui River, local iwi are trialling reconstruction of "utu piharau" (Potaka, 2016). In the Catlins (Southland Region) "whānau" (family) are connecting young people with customary fishing practices and sites (Blair "whānau" and the Rangitahi Tumeke programme).

Developing management strategies for pouched lamprey are currently hindered by the limited understanding of their ecology. For example, the first spawning site for a Southern Hemisphere lamprey species was only documented in 2013 (Baker et al., 2017). To address knowledge gaps and inform management and future bylaws for the Waikawa/Tuma Toka Mātaitai reserve by local Māori "kaitiaki", ecological research is currently being conducted in the Waikawa River (Baker and Kitson, 2016; Kitson et al., 2018). Waikawa "kaitiaki" are working with the National Institute of Water and Atmospheric Research Ltd to identify the spawning habitat used by "kanakana". This research is suggesting the microhabitat utilised by pouched lamprey is consistent across streams, with fish choosing enclosed cavities that minimise predation, with good water flow and that have hard surfaces for egg laying. Waikawa "kaitiaki" have also undertaken cultural monitoring and explored the use of DIDSON (acoustic cameras, Kitson et al., 2012) and larval bile acid (pheromone) samplers (Stewart and Baker, 2012; Kitson et al., 2018) as methods of assessing "kanakana" abundance. Sampling for "piharau"/"kanakana" pheromones has aided other Māori communities in determining the current distribution and relative abundance of this "taonga" in their tribal areas (Baker et al, 2016a, 2016b).

## Concluding remarks

Socio-cultural heritage associated with lamprey harvesting techniques and use for human consumption is present in almost all geographical regions where lampreys occur. Every year festivals that promote the consumption of lampreys and celebrate the annual fishing season are common in many countries (e.g., Portugal, Spain, Finland, Estonia, Latvia) and are responsible for an important income in certain regions Some traditions go back many centuries (e.g., Roman times in Europe, native people in North America and New Zealand), and include regional harvest, preservation and cooking methods. Modern times brought technological advances (e.g., synthetic fibres, outboard engines) that increased dramatically the fishing effort on commercially exploited lampreys (e.g., sea lamprey and river lamprey in Europe), contributing to the strong decline in population numbers observed in certain regions (e.g, Iberian Peninsula, England, France, Baltic countries), particularly in the second half of the 20th Century. Based on our review, habitat loss appears to be the main cause for severe declines in most lamprey populations worldwide, resulting in the collapse of the associated commercial fisheries (e.g., river lamprey in Finland, Sweden, Britain; sea lamprey in the Iberian Peninsula and in USA, Caspian lamprey in the Volga River). Extensive changes in watersheds during the 20th Century (e.g., dam construction, river flow regulation, pollution) were responsible for the degradation and loss of a substantial lamprey habitat (e.g., 80% loss in the Iberian Peninsula for sea lamprey, Caspian lamprey in the Volga River).

For most lamprey species in their native range, management actions have been implemented to restore habitats (e.g, construction of fish passes), increase population size (e.g., artificial reproduction and restocking) and establish sustainable management of the fisheries (e.g., fishing closures, quotas). However, in Russia, Arctic lamprey is considered a threat to salmon conservation and harvesting limits are set to control lamprey populations. Perhaps the best results come from case studies where an integrated socioeconomic and ecosystem approach is put in place, focusing on increasing the area of accessible suitable habitat through fish pass construction and, simultaneously adapting fishing regulations towards a sustainable harvest policy (Stratoudakis et al., 2016).

A subject that needs clarification is the actual fishing mortality in most major river basins. As Maitland et al. (2015) stresses, the low levels of current harvest relative to historic levels can be misleading. In fact, the proportion of a spawning population that is being harvested could be extremely high. Catching lampreys during their upstream migration, especially if fishing gears are set in physical bottlenecks that concentrate the spawning population, can result in exceedingly high fishing mortality. For example, in the Mondego River, estimates show a fishing mortality between 20% and 50% of the spawning population, and in certain years it can be even higher (P.R. Almeida, com. pers., 2020). Data for many lamprey species comes from reported commercial landings, but in some cases (e.g., sea lamprey in Portugal) official records are a clear underestimation of the real catch, mostly because of weak control of the product origin by the authorities (Stratoudakis et al., 2016, 2020). An estimate of the mortality associated with poaching is also needed in many river basins, IUU is a problem in several anadromous fisheries, especially in the case of lampreys (Andrade et al., 2007; Stratoudakis et al., 2020). Well-designed monitoring studies could reveal sources of mortality, the efficacy of management methods such as fishing regulations, and the efficacy of mitigation and restoration efforts (e.g., habitat restoration, fishing closures, artificial rearing and stocking). Here, good reference rivers with relatively pristine conditions would provide important insights for comparison purposes.

Apart from the Korean lamprey, anadromous lamprey species are the prime target of commercial and/or subsistence harvest, for which there are major knowledge gaps on the marine phase of their life cycles, namely, distribution at sea, stock structure, preferred hosts, and how climate change is increasingly impacting upon the distribution and availability of suitable hosts (Hume et al., this issue; Lucas et al., this issue). These unknown factors affect lampreys' population dynamics and are responsible for a huge amount of uncertainty in fishery/conservation management plans that were described in the previous sections of this review. We continue to act as if all the problems exist only in freshwater. Up to a certain point, this is true because the reduction in spawning and larvae rearing habitat, resulted in the collapse of many lamprey populations worldwide. Basically, we have assumed that conditions were not changing much in the marine environment, a common mistake with regard to the management of diadromous fishes (ICES, 2015, 2018).

Declining trends in survival at sea have been observed for many anadromous fish stocks, driving some to a threatened status (e.g., ICES, 2018; Olmos et al., 2018). In several cases this has been linked to climate-driven changes that make marine ecosystems less favorable (e.g., Mills et al., 2013). Anadromous lampreys may be especially sensitive to such ecosystem changes because successful completion of their life cycle requires matching their distributions with those of hosts, and with required seasonal conditions in freshwater, estuarine and marine zones (Hume et al., this issue). Besides, drought years are becoming more frequent, particularly in the drier parts of the distribution for each species. This can affect the ability of lampreys to find rivers suitable for spawning (sea lamprey, P.R. Almeida, unpublished data; Pacific lamprey, Stewart Reid, unpublished data), and so it is essential that we learn more about the environmental cues that trigger the spawning migration at sea, and also the fate of lamprey that do not find rivers in drought years.

Despite the fact that in the last decades the rate of freshwater habitat modification has slowed in many regions (e.g., Europe, North America), lamprey landings from commercial fisheries continue to decline, but with abrupt annual fluctuations. This raises conservation concerns, and the first management action to be put in practice is reduction of fishing effort, hoping to attenuate fishing mortality. Curiously, in most of the commercial lamprey fisheries there is no estimate of the fishing mortality, or even how harvest affects lamprey abundance in a specific river basin, or on a group of watersheds draining to the same coastal region. The fact that the identification of stock management units is complicated by the lack of observed philopatry in lampreys (Docker et al., 2015; Mateus et al., this issue; Quintella et al., this issue), makes regional management even more difficult. However, some local adaptations and similarities between lampreys from geographically close rivers indicate a lack of random dispersal after entering the sea (e.g., Lança et al., 2014). Hence, identification of sources and sinks of lamprey production would allow for prioritization of protection/management measures that will have the greatest effect on species persistence and/or sustainable harvest strategies.

Finally, in addition to the needs for ecological knowledge, and reliable fisheries data, by which to manage lamprey exploitation, it is also necessary to collect cultural information and preserve the traditions of lamprey fishing and use. With the loss of indigenous lamprey fishing will come a loss in motivation to protect and conserve these species. Outreach activities are essential to promote the protection of the ecological and cultural values of lampreys and the understanding of their vulnerability.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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